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FUNGI, LICHENS AND MOSSES IN RELATION TO VASCULAR PLANT COMMUNITIES IN EASTERN WASHINGTON AND ADJACENT IDAHO

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INTRODUCTION

This study was undertaken to discover what differences there might be in species composition, relative abundance, substratum preference, and spring and autumn appearance of the fruit bodies of macroscopic fungi in six associations of four major vegetation zones. Lichens and bryophytes were studied in the same series of plots to determine the extent to which the distribution of these plants is correlated with the grassland, shrub and forest communities under observation. The field work included three spring, one summer and four fall seasons of study in eastern Washington and adjacent Idaho. The literature of the synecology of the fungi so far as available to date has been reviewed separately (Cooke 1948, 1953).

PLOT LOCATIONS AND DESCRIPTIONS

Eighteen plots were studied, these being equally divided among six associations. To obtain wide geographic variation within each association, the three stands of each association were spaced as far apart as possible within a 150 mi. radius of Pullman, Washington.

In the text and in the tables these plots are mentioned in code. The following descriptions are arranged in the same order as the plots are presented in the tables. The associations are arranged in ascending order should they have occurred on a single slope. Theoretically the sequence is an altitudinal one, although many of the plots are at about the same altitude. The components N, C and S of the code symbols refer to the northernmost, central and southernmost of the three stands used in each association. More complete descriptions of the associations may be found in Daubenmire (1942, 1952). Plot locations are shown on the accompanying map (fig. 1).

I. *Festuca idahoense-Agropyron spicatum* Zone.

This vegetation zone, which characterizes the Palouse and Nez Perce Prairies, lies adjacent to the forested foothills along the western edge of the northern Rocky Mountains. The dominant grasses are *Festuca idahoense* Elmer and *Agropyron spicatum* (Pursh) Scribn. & Smith.

A. *Festuca/Symphoricarpos* Association. Remnants of this vegetation occur mostly on land unfavorable to cultural practice.

FN. South side of State Route 3, 0.2 mi. east of U. S. Highway 195 at Donahue near Rosalia, Whitman Co., Washington. Station lies in a climax prairie on a steep north facing slope, elevation 2300 ft., T.20 N., R.43 E., S.26. The area is surrounded by cultivated fields and apparently has not been grazed for at least 5 years.

FC. East edge of The State College of Washington Campus, Pullman, Whitman Co., Washington. Station lies in a remnant of climax prairie preserved by

FIG. 1. Map of Eastern Washington and adjacent Idaho showing locations of plots (indicated in code), important communities and counties.

the college on a south facing slope at an elevation of 2500 ft., T.14 N., R.45 E., S.5.

FS. 2 mi. east of Mohler, south side of State Route 12, Lewis Co., Idaho. (Between the towns of Nez Perce and Craigmont.) Station lies in a climax prairie on a gentle north facing slope, elevation approximately 3200 ft., T.34 N., R.1 E., S.22. Small area surrounded by cultivated fields but undisturbed for several years.

B. *Symphoricarpos/Festuca* Association. This association is dominated by the deciduous shrubs *Symphoricarpos albus* (L.) Blake and *Rosa spauldingii*, Crepin and is common in patches on north slopes throughout the *Festuca-Agropyron* Zone.

SN. Adjacent to FN in a climax thicket on a northwest facing slope between a country road and a field.

SC. Adjacent to FC in a climax thicket on the north slope.

SS. 3.2 mi. west of Mohler, northwest side of State Route 12, Lewis Co., Idaho, in a near-climax thicket on a southwest facing slope at approximately 3200 ft., T.34 N., R.1 W., S.24. Although this station lies below a plowed field it has been relatively undisturbed for the last several years.

II. *Pinus ponderosa* Zone. The tree that dominates this zone is *Pinus ponderosa* Dougl. Only the two principal associations were studied although several minor ones are also included in this zone.

A. *Pinus ponderosa/Agropyron* Association. The ground cover is made up of the same grasses that dominate the grassland zone.

PaN. 2.2 mi. north of the Northern Pacific Railroad overpass north of Spangle on east side of U. S. Highway 195, Spokane Co., Washington; open climax forest on a gravelly till plain; elevation 2000 ft., T.23 N., R.43 E., S.17. Undisturbed for a number of years.

PaC. South side of Paradise Ridge, Latah Co., Idaho; open climax forest on a south slope; elevation 3000 ft., T.39 N., R.5 W., S.27. Undisturbed throughout most of the period of study; in the early fall of 1949 a swath was cut through the plot to install an electric line.

PaS. 4.8 mi. south of Stites, Idaho Co., Idaho; on steep west-facing slope of canyon along the south fork of the Clearwater River; open climax forest; elevation approximately 1500 ft., T.31 N., R.4 E., S.9.

B. *Pinus ponderosa/Symphoricarpos* Association. In this phase of the pine forest the same shrubs comprise the undergrowth as dominate the shrub association in the preceding zone. It occurs on what appear to be moister habitats than the preceding association, especially on north facing slopes.

PsN. Along California Creek near Valley Ford, 0.2 mi. southeast of the Palouse Highway, Spokane Co., Washington; moderately open climax forest in a shallow valley; elevation 2000 ft., T.24 N., R.44 E., S.33. The plot is relatively undisturbed although at certain times there are evidences of its use as a bivouac for a small Boy Scout troop.

PsC. South side of a county road approximately ½ mi. southeast of Fischer's ranch on a tributary of Union Flat Creek, Whitman Co., Washington; moderately open climax forest on a north facing slope; elevation 2500 ft., T.15 N., R.44 E., S.31. The plot adjoins a small abandoned apple orchard into which cattle occasionally come for shade. While there are old cattle paths across the shrub thickets in the plot there is no evidence of recent disturbance of the vegetation. In the immediate vicinity, but not on the plot itself, is a campfire site apparently used every fall by picnicking parties.

PsS. East side of U. S. Highway 95 at north edge of Winchester, Lewis Co., Idaho; moderately open climax forest on a well drained upland; elevation approximately 3200 ft., T.34 N., R.2 W., S.31. The plot adjoins a park used by the people of Winchester. There was evidence of its having been used as a pasture for one or more horses, and as a play woods for local children. The vegetation was relatively undisturbed. On Nov. 2, 1947, when most fungi were observed, there was no damage to them other than that caused by our investigation.

III. *Pseudotsuga taxifolia* Zone. Climax stands in this zone are dominated by *Pseudotsuga taxifolia* var. *glauca* (Mayr.) Sudw. Where this zone adjoins the *Pinus ponderosa* Zone, *Pinus ponderosa* is the chief seral tree species because of past fires.

A. *Pseudotsuga taxifolia/Physocarpus* Association.

DN. 8.2 mi. north of the Northern Pacific Railroad overpass north of Spangle on the west side of U. S.

Highway 195, Spokane Co., Washington; dense, near-climax forest, on a level bench at the bottom of an east-facing slope; elevation 2000 ft., T.24 N., R.45 E., S.17. Throughout the period of study ponderosa pine trees were removed from this forest for cordwood. Few trees were removed from the plot itself and there was no evidence of disturbance to the fungi.

DC. West end of Thatuna Ridge, ½ mi. west of U. S. Highway 95, Latah Co., Idaho; dense, near-climax forest on a north slope; approximately 3100 ft. T.40 N., R.6 W., S.23. The only disturbance to this plot was caused by storms which have caused considerable windfalls in the last two years.

DS. 4.8 mi. east of Lenore on the south side of State Route 9, Nez Perce Co., Idaho. Dense, near-climax forest, on a steep north-facing slope near the bottom of the Clearwater River Canyon, 900 ft., elevation, T.36 N., R.1 W., S.4. No disturbance to the vegetation on this plot was noticed during the progress of the study but earlier young trees had been removed apparently for use as Christmas trees.

IV. *Thuja-Tsuga* Zone. In this zone the more characteristic trees are *Thuja plicata* Donn. and *Tsuga heterophylla* (Raf.) Sarg. There are four principal associations in this zone of which only the lowest is considered in this study.

A. *Abies grandis/Pachistima* Association. *Abies grandis* (Dougl.) Lindl. is the outstanding climax dominant while *Pseudotsuga taxifolia* var. *glauca* approaches climax status. Seral trees observed include *Pinus ponderosa, Larix occidentalis* Nutt., and *Pinus contorta* var. *latifolia* Engelm.

GN. One mi. east of Springdale, southwest side of U. S. Highway 395, Stevens Co., Washington; dense, near-climax forest on a northeast-facing slope; elevation 2200 ft., T.30 N., R.40 E., S.35. Trees present include *Abies grandis, Pseudotsuga taxifolia* var. *glauca, Larix occidentalis, Pinus ponderosa* and *Pinus contorta* var. *latifolia*. Vegetation apparently undisturbed during the study although it was evident that at least one horse had used a trail through the plot.

GC. One mi. north of State Route 8 along Dry Creek, Latah Co., Idaho; dense, near-climax forest on an east-facing slope; elevation approximately 3000 ft., T.40 N., R.3 W., S.25. Trees present include *Abies grandis, Pseudotsuga taxifolia* var. *glauca, Larix occidentalis, Pinus contorta* var. *latifolia* and *Pinus ponderosa*. No apparent disturbance to this forest, during the study or for several years prior thereto.

GS. One-half mi. up Rackliff Ridge Trail from Rackliff Creek Public Camp Ground, along the Selway River, Nez Perce National Forest, Idaho Co., Idaho; young, dense, near-climax forest on a south-facing slope at about 2100 ft., T.32 N., R.8 E., S.20. The forest is composed exclusively of young trees of *Abies grandis* and *Pseudotsuga taxifolia* var. *glauca* although near the plot are mature trees of *Pinus ponderosa*. Although the trail passes through the plot there is no apparent disturbance to this forest.

METHODS OF COLLECTION

Fungi

Because of the distances involved in getting from one plot to another it was impossible to visit the whole series in one day or even in a two day trip. To space the trips to the plots evenly and to get in three trips to each plot during a season it was decided to visit the six plots on the southern route on one week end, the four on the eastern route on another week end, and the six on the northern route on another week end. While the two plots on the Campus at Pullman were visited the day before and the day after each of the trips for moisture stick determinations, fungi were recorded only at the times of the eastern route trips.

Three trips were made to most plots in the fall of 1946, 1947 and 1948, and in the spring of 1948 and 1949. Two trips were made to most plots in the spring of 1947. One trip was made to each plot in the summer and fall of 1949. Occasionally it was not possible to reach some of the plots because of road conditions.

Plots used in this study were not always square but attempts were made to study areas approximately thirty meters on a side. Some oblong plots of the same area were also used. The shape of the plot depended on the shape of the stand in which it was located.

At each visit to a plot an attempt was made to collect all specimens of fungi observed. When too many fruit bodies were present to collect all of them in the period of time available, a count or estimate was made of those not collected. With extremely abundant species, notably certain of *Marasmius* and *Mycena*, estimates rather than counts were made. Estimates for the entire plot were then based on counts of fruit bodies on a restricted area.

Comparative studies of paired plots are needed to see whether or not picking fruit bodies has an adverse effect on the mycelium by permitting the entry of parasitic organisms.

Lichens and Bryophytes

On those visits to the plots when the fungi were poorly developed, mosses and lichens were collected with the idea of obtaining as many species as possible from the sample areas. Species occurring on tree or shrub trunks or branches, on the soil, on stones and on rotting wood were searched for. No attempt was made to obtain quantitative sociologic data on these groups.

ECOLOGIC AND SOCIOLOGIC OBSERVATIONS

Soil Studies

To determine whether any factor or group of factors in the physical or chemical composition of the soil could be considered as affecting the distribution of fungi found, a series of analyses was made. Soil was obtained from each plot as a composite sample of the upper 6 in. from several locations on the plot. They were studied according to techniques which give

TABLE 1. Results of Soil Analyses

Plot	Parent Material	Percentage of Soil Separates†			Hygroscopic Coefficient %	Field Carrying Capacity %	Volume Weight	pH	Exchange Capacity m.e./100 Grams Soil
		Sand† Gravel	Silt	Clay					
FN	Loess on residual	38	60	2.5	5.4	28.5	.87	6.8	34.6
FC	Loess	33	61	6	4.6	23.5	.98	7.1	28.3
FS	Loess	22	69	9	4.8	20.1	1.03	6.3	25.1
SN	Residual	25	66	9	5.4	23.5	.83	6.5	28.0
SC	Loess	24	69	8	4.7	26.5	.85	6.6	30.2
SS	Loess on residual	23	67	10	6.3	31.6	.73	6.8	30.8
PaN	Stony till	47	48	5	2.7	15.0	1.22	6.2	17.2
PaC	Residual granitic	33	54	13	3.5	11.9	1.17	6.2	15.7
PaS	Very rocky, colluvial	57	40	3	9.1	29.5	.78	6.3	36.9
PsN	Alluvial	41	50	9	8.5	36.1	.61	5.7	24.0
PsC	Loesso-colluvial	21	69	10	5.1	21.7	.90	6.3	20.7
PsS	Loess on residual	27	60	13	6.5	32.3	.78	6.1	30.7
DN	Residual	40	53	7	5.1	25.6	.63	6.0	30.3
DC	Loess on residual	35	53	12	5.1	25.1	.82	6.7	26.2
DS	Residual granitic	39	41	10	6.8	19.6	1.02	6.7	26.3
GN	Glacial	30	60	9	4.9	37.4	.76	5.8	26.1
GC	Residual	31	58	11	6.3	36.2	.58	6.4	32.7
GS	Residual granitic	73	21	6	2.4	19.2	.97	6.9	13.9

Plot	Parent Material	m.e. Exchangeable Calcium/100 Grams Soil	Per cent of Exchange Complex Saturated by Ca	Soil Nutrients in Pounds/acre 6 in. Soil			Easily Oxidizable Organic matter Expressed as m.e. $KMnO_4$ per gram used	Per cent Total Nitrogen	Nitrification Capacity as ppm N after 10 weeks
				Ca	K	P			
FN	Loess on residual	16.5	48	4800	480	48	11.3	.32	41
FC	Loess	18.0	64	4800	120	36	7.6	.24	48
FS	Loess	12.7	50	3640	360	72	2.8	.17	38
SN	Residual	14.2	51	4800	480	36	9.9	.28	106
SC	Loess	11.7	38	4800	480	60	8.7	.29	77
SS	Loess on residual	22.8	63	4800	600	60	11.4	.40	119
PaN	Stony till	7.9	46	2880	360	60	0.4	.079	13
PaC	Residual granitic	8.4	53	2880	240	48	2.6	.14	31
PaS	Very rocky, colluvial	20.7	56	4800	360	72	11.4	.32	94
PsN	Alluvial	10.8	45	2880	480	30	19.2	.31	6
PsC	Loesso-colluvial	10.1	49	2880	360	48	1.8	.15	47
PsS	Loess on residual	17.3	57	4800	360	48	10.1	.25	45
DN	Residual	14.0	46	2880	360	36	9.0	.17	75
DC	Loess on residual	12.9	49	4800	480	48	6.3	.19	52
DS	Residual granitic	15.7	60	4800	480	72	8.6	.27	41
GN	Glacial	12.1	46	2880	600	60	12.5	.20	45
GC	Residual	14.7	45	3640	600	30	14.7	.27	84
GS	Residual granitic	7.2	52	1920	120	42	2.7	.10	43

†Gravel and Sand >2.0-0.02 mm; Silt 0.02-0.002 mm; Clay 0.002-0.001 mm.

only approximate results. Results are presented in table 1. In trying to match total number of fungus fruiting bodies collected or recorded on each plot with the several types of data obtained from this soil study no correlation was obtained either within the six associations or between them.

These results indicate that in this series of relatively undisturbed sample plots there is insufficient difference in the soil characteristics studied to explain features of fungus distribution.

CLIMATIC FACTORS

McMinn (1952) found that in the area covered by this study, "where precipitation is mostly in the winter and summer drought is normal, different plant associations are correlated with different extents of soil drought." This condition is probably critical for the fungi.

It is well known that abundant moisture is required for the production of fungal fruit bodies, especially the large, fleshy ones, since up to 95% of the weight

of a mushroom is water. Not only must the water be present in large amounts at lower levels where the mycelium can absorb and conduct it to the fruit initial and the fruit body, but moisture must be available in the fruiting region: the upper few centimeters of the soil, duff and litter through which the fruit body is raised from the mycelium to the surface of the ground, and the few centimeters of air next to the ground surface in which these fruit bodies exist while discharging their spores.

MACROCLIMATE

The usefulness of meteorologic data from the several weather stations in the area was limited although charts prepared from these data indicate fairly consistent trends throughout the area for different seasons. Meteorologic data were chosen to show the overall weather picture for the area in which the plots are located. Figures 2, 3, 4 and 5 summarize these data.

MOISTURE STICK DETERMINATIONS

General climatic conditions obtained from weather stations cannot give an indication of the climatic conditions on all of the plots. It was impractical to use recording instruments on each plot to obtain data for microclimatic comparisons, because of the prohibitive cost of a large number of instruments and the difficulty of servicing them regularly.

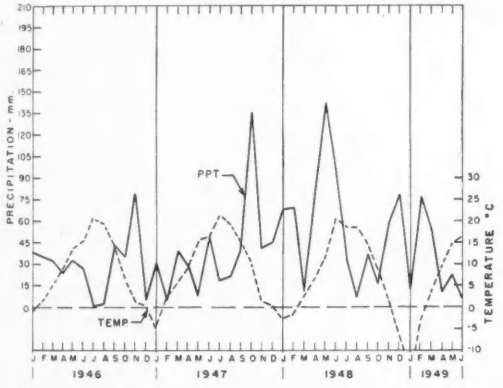

FIG. 2. Precipitation and temperature: Spokane, Washington. Representative of plots FN, SN, PaN, PsN, DN and GN.

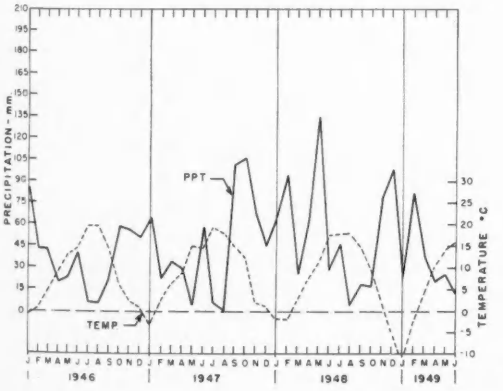

FIG. 3. Precipitation and temperature; Pullman, Washington. Representative of Plots FC, SC, PaC, PsC, DC and GC.

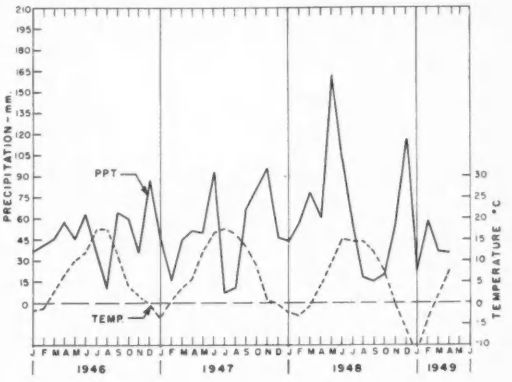

FIG. 4. Precipitation and temperature: Winchester, Idaho. Representative of Plots FS, SS and PsS.

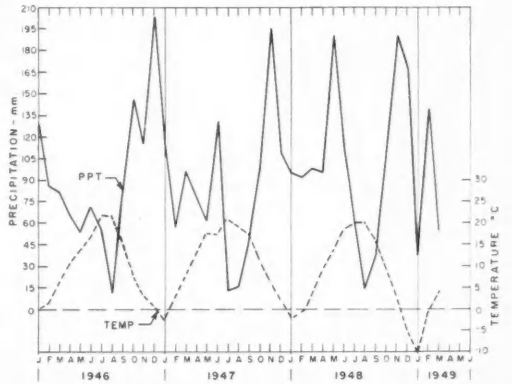

FIG. 5. Precipitation and temperature: Fenn Ranger Station, Selway Valley, Idaho Co., Idaho. Representative of Plots PaS, DS and GS.

To obtain a comparison of moisture conditions at and near the surface of the ground a modification of the Gisborne (1936) fuel moisture stick was used. In the present study these were made of western white pine wood. Four pieces 1 cm^2 and 50 cm long were held 1 cm apart with pieces of the same wood 7 cm long and 1 cm^2 nailed crosswise near each end. The units were numbered with India ink, stained brownish with water-soluble stains for camouflage purposes, oven-dried and weighed. Two units were placed on the soil surface, with the short crosswise members lowermost, in what were estimated as average positions of exposure on each plot at the beginning of each season. On each trip these were weighed in the field. At the last visit after weighing they were returned to the laboratory for drying, weighing and interpolation of the dry weight of the unit at the time field weights had been taken. This was con-

sidered necessary because the same sticks were used throughout the exposure periods and weight was gradually lost because of leaching, degradation and mechanical injury. Weights obtained in the field included the dry weight of the stick plus the moisture accumulated from precipitation, dew, frost or absorption from the soil.

The ratios obtained by this technique are probably superior to instantaneous measurements of relative humidity, as the water content of the sticks reflects the net effect of the conditions over a period of hours.

Since two or three readings were made in each season, only trends can be indicated and these are best recorded here by presenting seasonal averages for the four seasons in which the technique was used. In table 2 the "absolute" for each season represents the average of the amount of water present in the sticks at plot FC for each season.

TABLE 2. Moisture relationships determined by moisture sticks.

Station	Fall 1947	Spring 1948	Fall 1948	Spring 1949	Average
Absolute*	40.52	16.02	15.28	6.83	19.66
FN	1.83	1.36	3.3	1.58	2.02
FC	1	1	1	1	1
FS	0.86	1	1.2	1.83	1.22
SN	2.28	1.34	4.28	2.48	2.6
SC	2.07	1.09	2.4	1.25	1.96
SS	1.12	2.45	4.7	3.05	2.83
PaN	1.13	1.02	1.26	1.07	1.12
PaC	2.73	1.66	4.55	1.2	2.79
PaS	0.6	1.02	1.98	1.37	1.26
PsN	2.94	2.74	3.49	1.16	2.58
PsC	0.9	2.61	1.54	2.27	1.83
PsS	1.6	1	2.9	3.72	2.31
DN	1.6	1.26	1.89	1.26	1.5
DC	2.01	1.46	3.67	1.5	2.16
DS	1.7	2	2	2.06	1.94
GN	1.78	1.99	2.22	1.98	1.99
GC	2.83	1.64	4.14	1.58	2.55
GS	0.5	1.9	2.5	....	1.63

*Average water content in grams of two sets of moisture sticks at FC.

The detailed results of the moisture stick study, upon which table 2 is based, indicate that as the season progresses in the fall more moisture becomes available, as it advances in the spring less moisture is available at the ground surface. Readings should be made daily to be of value beyond indicating trends.

SOIL TEMPERATURE

At each visit to each plot in 1948 and the spring of 1949 the temperature of the soil at 2 dm depth was taken with a laboratory thermometer which was permitted to come to equilibrium with the soil for at least 10 minutes before it was read. As a basis for comparison a thermometer was maintained at 2 dm in an artificial grassland plot 1 mi. west of Pullman. This was read by a co-operator at intervals throughout the days on which trips to the plots were made. If the times at which readings were made did not coincide, interpolations and extrapolations were made to obtain comparisons so that all temperature measurements made at the field stations could be referred to the standard station. The temperatures are reported in table 3 as the average of the differences between the field and the base readings by associations.

TABLE 3. Average temperature differential between associations and the standard station.

Association	Spring 1948	Fall 1948	Spring 1949
F	−0.7	1.7	1.6
S	−1.1	−0.7	−1.8
Pa	−0.7	2.2	−0.01
Ps	−1.9	−0.1	−1.1
D	−1.9	1.4	−2.1
G	−3.4	0.06	−4.1

Readings were taken at 2 dm to eliminate some of the rapid fluctuation of temperature in the upper few centimeters of soil which occur in well insolated areas such as found in some of the plots. It is possible that this depth was somewhat below that of most of the actively growing mycelium in the soil so that the data have only comparative value.

The results of the temperature study indicate a progressive cooling of the soil in the fall, a progressive warming of the soil during the spring. Table 3, showing the total difference between temperatures throughout the association in each season and the temperature of the standard station, indicates that, with few exceptions, in the spring the plots are progressively cooler toward higher elevations. McMinn's studies (1952) have shown that the same gradient persists through midsummer. In the fall the relationships are very irregular. Precipitation in the form of snow at the end of each fall season prevented observation of the minimum soil temperature at which fleshy fungi will fruit in the altitudinally higher plots. Even though air temperature was below freezing, as indicated by frozen fruit bodies, soil temperature was above freezing since fruit bodies continued to be formed up to the time of persistent snow cover. These frozen fruit bodies thawed in the daytime and sporeprints could be obtained from them in the laboratory indicating no loss of function during freezing.

PRECIPITATION—TEMPERATURE CORRELATIONS

Monthly average temperature, total monthly precipitation, and the relation between these factors as represented by the ratio: precipitation in millimeters to degrees Centigrade plus ten, were compared as a possible source of correlation. The data (fig. 6) were obtained from averages of Weather Bureau records reported from Spokane and Pullman, Washington, and Nez Perce and Orofino, Idaho. There was little, if any, correlation between monthly temperature and precipitation and spring fruiting ex-

pressed as total numbers of fruit bodies. On the other hand, fruiting in the fall season can be more easily correlated with precipitation or the ratio between precipitation and temperature than with temperature alone. In the fall of 1946 early season precipitation leveled off, apparently preventing the rich development of fruit bodies observed the following fall season. In the fall of 1947 rain started early and continued throughout the season. In the fall of 1948 there was a relatively dry early season followed by late precipitation mostly in the form of snow. Air temperatures were somewhat higher in the fall of 1947 than in either the fall of 1946 or 1948. Soil temperature was recorded only in the fall of 1948 so this factor cannot be used in a comparative study. Moisture sticks showed much higher moisture contents through the season of 1947 than 1948.

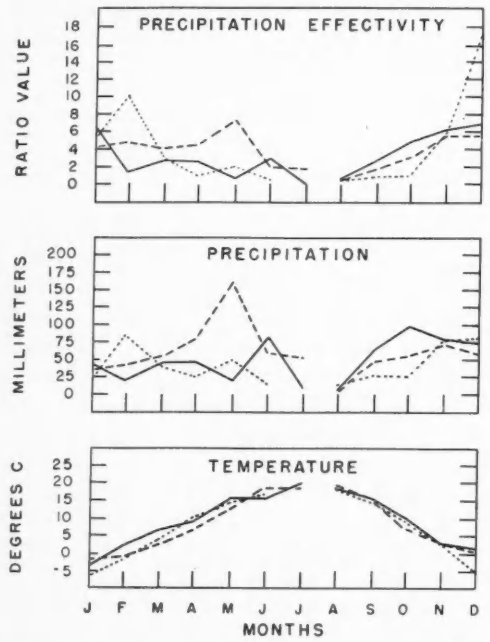

FIG. 6. Correlation of Numbers of Fruiting Fungi with Temperature, Precipitation and Precipitation Effectivity. In the three diagrams best fruiting season is represented by a solid line, medium by a broken line and poorest by a dotted line. In the spring season curves 1947 is solid, 1948 broken and 1949 dotted. In the fall season the solid curve represents 1947, the broken line 1946 and the dotted line 1948.

Records from appropriate Weather Bureau stations were studied in an effort to correlate fruiting with temperature and precipitation. For one plot in each association temperature and precipitation data were obtained from records of the nearest station for the three weeks preceding each date on which fungi were collected throughout the three-year study period. Data were changed to the metric system for both temperature and precipitation. For all spring and fall seasons the collecting dates were aligned in one series of decreasing numbers of species obtained from each plot. These were compared with mean temperature for the preceding one-week, two-week and three-week periods, and with total precipitation for the same periods. An additional type of correlation was based on the interaction of these values and was determined first by adding the mean temperature and total precipitation, second by subtracting the mean temperature from the total precipitation. The only correlation which this type of analysis suggested was found in the spring season in plots FS and SS.

An additional type of correlation was based on alignment of the collection dates in descending order by numbers of species collected on each date for spring and autumn seasons. The ratio precipitation/temperature plus ten was used in an attempt to get a correlation. In this case no correlation was found in fall seasons, but for three plots spring correlations were found. In FS correlations for the preceding one and two weeks were fair although for the preceding three weeks they were poor. In SS for the preceding one week there was no correlation, correlation for the preceding two weeks was fair and good for the preceding three weeks. In PsS for the preceding one week correlation was fair while for the preceding two and three weeks correlation was good. Because of the erratic nature of these correlations they are not considered important since in no other cases in the 180 possibilities was there any harmony between these factors and the numbers of species of fungi obtained. This lack of correlation can be attributed to several factors. The trips to the plots were too few in number and too far apart to obtain complete information concerning the numbers of species fruiting in the plots. The weather information obtained from centralized, standardized, weather stations probably does not indicate the conditions of temperature and precipitation on the plot especially as they affect the fruiting of fungi. Another consideration that may well be significant in this analysis is the fact that in the fall of 1947 conditions permitted very abundant fruiting. As a result of the overabundance of fruiting in this season it is possible that the mycelium of many of the species became exhausted. During the two years following that season it is possible that the mycelium had not yet recovered despite proper conditions for abundant fruiting.

In the fall of 1947 the plots yielded a larger crop of fungus fruit bodies than in any other season in which they were studied. This is correlated with the fact that there was a greater amount of precipitation than reported for any preceding year for which climatic data have been recorded in the area. Because of this seasonal irregularity statistical analyses of the populations encountered could not be made.

Fruiting increases during the fall, in spite of occasional freezing of fruit bodies, until the time of permanent snow cover although the soil cools off, while in the spring fruiting of soil species appears to be affected by rains and increasing air temperature rather than by temperature of the soil.

MICROBIOLOGICAL ACTIVITY

Although this study concerned primarily the larger fungi, or macromycetes, a few analyses were made on micromycetes in the soils.

From the soil samples collected in the spring of 1948 one gram portions were plated out in potato-dextrose agar. Counts of mold colonies developing on these plates were made and representative colonies were transferred to culture tubes for further study. The species thus obtained number 48 and are listed in the composite fungus list (Table 4A, B).

The plate counts listed in table 5 show that more colonies were usually obtained from forest than grassland soils by this technique in this season, but most of the species are ubiquitous.

To determine whether there was any difference among the plots and the associations in respect to micro-organisms present in the upper soil layer and their reaction to special substrata, strips of unbleached cotton duck and undyed wool charmeen were buried in the soil of each plot in the spring of 1949. This was suggested by a technique used in Switzerland by Richard (1945). Twenty-four standard 1 x 6 in. strips of each type of cloth were placed approximately 1 cm deep in rows in each plot on the first trip of the season to the plot. On the second trip, two to three weeks after burial, half of the strips were harvested and the second half of the strips were harvested five to six weeks after burial. The strips were air-dried and tested along with strips which had not been buried, the latter serving as controls with their tensility considered as 100%. Tensile strength was measured at the Philadelphia Quartermaster Depot using a Scott tester.

Beyond making a few fresh-water mounts, isolation of only two organisms from these materials has been attempted. These two, *Thielavia sepedonium* Emmons and *Microsporum gypseum* (Bodin) Gniart & Grigorakis, fruited abundantly on the cloth before the final harvest causing complete degregation of the wool charmeen fibers resulting in complete loss of tensile strength of the strips on which they grew.

Microbiological activity is compared in table 5 where results from the degradation trial, the plate counts, and the collection of macroscopic fruiting fungi are listed for comparison.

Since Thielavia and Microsporum were obtained by means of soil burial of cloth strips but not by the plating technique the test indicated the possibility that perhaps many more organisms could be isolated from the soil by placing in the soil on the site certain differential media such as cellulosic or proteinaceous materials more readily than by plating techniques.

It was hoped to discover if consistent differences existed between soil microbiological activities among the plots and associations. Results of the preliminary study indicate that the treeless plots have a series of organisms which tend to be more active on cotton or cellulosic materials than are the microorganisms of the other plots, or that the organisms may be the same but less effective under forest temperature conditions. Beyond this no special trends were shown.

TABLE 4. Distribution and habitats of cryptogams in study plots. The species of fungi, lichens and bryophytes are listed according to their occurrence on the plots with certain habitat data. Symbols used in tables 4A and 4B are explained below.

Ecologic Status: (Parker-Rhodes, 1951)
Prev.—Prevalent: Three or more records in any one year.
Subvalent:
App.—Apposite: At least two records in at least one year.
Prep.—Preposite: Only one record in any one year.

Habitat: Fungi
C—Saprobic (growing on dead organic matter) on cones—conigenic without regard to host.
D—Coprophilous—Saprobic on dung of various kinds and on owl pellets.
F—Pathogenic on fungi without regard to host.
G—Saprobic on the ground—most of the fleshy pileate species belong here, including mushrooms, etc.
GM—On the ground—suspected of having mycorrhizal relations with trees on the plots.
H—Hypogaeous—mycorrhizal or not.
L—Saprobic on litter and duff.
M—Found on living mosses—biologic relationship uncertain.
P—Pathogenic on living plants without regard to host.
P?—Usually considered pathogenic but relationship uncertain at time of collection.
PD—Pathogenic at some stage of cycle but found on dead plant tissues.
S—Soil molds.
SC—Soil molds isolated on cloth strips buried in soil.
T—Perthogens—found on dead parts of living trees.
W—Saprobic on rotten woody material of all kinds.

Habitat: Lichens and Bryophytes
B—Bark (unidentified).
C—Conifer Bark.
D—Deciduous Plant Bark.
G—Ground.
R—Rocks and Stones.
W—Wood.

Habit:
L—Leaf spots.
M—molds.
SM—Slime molds.
P—Pileate—with the following texture classes:
T-1—Ephemeral, lasting only a few hours.
T-2—Fleshy, putrescent after a few days.
T-3—Gelatinous, putrescent or reviving.
T-4—Cartilaginous or subcoriaceous, reviving after drying but short-lived; or, in the case of epigaeous Gasteromycetes, remaining of normal appearance until after release of all or most of the spores.
T-5—Coriaceous, leathery, woody or carbonaceous, reviving after short droughts or overwintering, but not living more than one or two seasons.
T-6—Perennial, as indicated by micro- or macro-scopic hymenophoral layers.

Year, Season and Trip Classes:

Year Classes:

A. 1946 Only.	I. 1947-1949.
B. 1947 Only.	J. 1948-1949.
C. 1948 Only.	K. 1946-1947-1948.
D. 1949 Only.	L. 1946-1947-1949.
E. 1946-1947.	M. 1946-1948-1949.
F. 1946-1948.	N. 1947-1948-1949.
G. 1946-1959.	O. 1946-1947-1948-1949.
H. 1947-1948.	

Season Classes:

A. Spring Only.	E. Fall and Spring.
B. Summer Only.	F. Fall and Summer.
C. Fall Only.	G. Spring, Summer and Fall.
D. Spring and Summer.	

Trip Classes:

A. First of a Season.	E. First and Third.
B. Second of a Season.	F. Second and Third.
C. Third of a Season.	G. First, Second and Third
D. First and Second.	

Numbers—Counted or estimated. Fewest, Average and Largest are given in that order. Based on total for year, season and trip classes for each species.

Volumes—Average per collection. Least, Average and Largest volumes are given in that order in CM^3 for each species for which this value could be obtained.

Distribution Classes:

Association:
F—*Festuca/Symphoricarpos* Association.
S—*Symphoricarpos/Festuca* Association.
Pa—*Pinus ponderosa/Agropyron* Association.
Ps—*Pinus ponderosa/Symphoricarpos* Association.
D—*Pseudotsuga taxifolia/Physocarpus* Association.
G—*Abies grandis/Pachistima* Association.

Plot:
N—Northern Plot.
C—Central Plot.
S—Southern Plot.

TABLE 4A. Distribution of Cryptogams through Study Plots

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Mycena vitrea	G																	
Coprinus 20823	G																	
Lepiota 21219	G																	
Marasmius 21698	G																	
Puccinia hieracii	P																	
Penicillium (*Cyclopium* Ser.)	S																	
P. purpurascens	S																	
Rhodophyllus 21724	G																	
Agaricus campestris		G																
Rhodophyllus 22712		G																
Tricholoma 24869		G																
Ramularia heraclei		P																
Heterosporium allii v. *sisyrinchii*		T																
Pullularia pullulans		S																
Geotrichum candidum		S																
Pestalotia sp.		S																
Penicillium lanosum		S																
P. crustosum		S																
P. simplicissimum		S																
Galerina hypnorum ss. Lange			G															
Rhodophyllus 19782			G															
Rhodophyllus 21388			G															
Conocybe siliginea			G															
Omphalina 19787			G															
Cladaria amythestina			G															
Psilocybe coprophila			D															
Tricholoma 21381			G															
Mycena mauritanica			G															
Tricholoma 21382			G															
Isaria sp.			D															
Pucciniastrum goeppertianum			P															
Ramularia cercosporioides			P															
Titaeospora detospora			P															
Claviceps purpurea	P			P														
Omphalina 19578	G			G														
Stemphyllium consortiale		S			S													
Omphalina 21721	G				G													
Puccinia vagans v. *gayophytii*		P			P													
P. grindeliae		P			P													
Uromyces probus		P			P													
Marssonina wyethiae		P			P													
Rhodophyllus 19783			G		G													
Marasmius epiphyllus			L		L													
Bovistella radicata	G		G			G												
Rhodophyllus 22203	G		G			G												
Phyllosticta fritillariae		P				P												
Macrosporium iridis		T	T			T												
Helotium herbarum		L				L												
Hainsia boreale			P			P												
Mycena atrocyanea	G		G					G										
Lycoperdon sp.	G							G										
Puccinia iridis	P	P			P			P										
Ramularia symphoricarpi		P			P				P									
Aspergillus flavus		S							S									
Clitocybe 21203			G		G			G	G									
Panaeclus acuminatus			G						G									
Phragmidium ivesiae	P	P			P			P		P								
White spored agarics	G		G	G	G	G		G	G	G	G							
Panaeolus campanulatus	G					G			G		G							
Lycoperdon pusillus	G	G										G						

TABLE 4A. Continued

Species \ Association	F			S			Pa			Ps			D			G		
Species \ Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Tubaria 21218	G	G		G	G							G						
Ramularia cynariae		P										P						
Lyophyllum 21696	G			G	G						G		G					
Collybia (misc.)	G						G						G					
Ustilago bullata	P						P		P				P					
Pleurotus 19791		G	G											G				
Bovista plumbea		G	G	G		G								G				
Omphalina sp.		G								G				G				
Puccinia crisii		P				P		P		P				P				
Phragmidium rosae-acicularis		P			P	P				P		P		P				
Puccinia difformis	P					P				P					P			
Penicillium thomii	S		S				S	S				S			S			
Stropharia aeruginosa	G	G		G	G	G					G				S			
Puccinia heucherae		P			P										G			
P. jonesii v. *jonesii*		P			P			P				P			P			
Panaeolus sp.		G		G		G		G	G	G	G		G	G	G			
Coprinus sp.		G				G		G		G	D			G	G			
Rhodophyllus sp.			G			G				G					G			
Collybia 19576	G				G		G			G	G				G	G		
Clitocybe 21112	G							G		G	G			G		G		
Trichoderma viride	S	S	S	S	S			S	SW	S			S	SW		S		
Penicillium spinulosum		S		S		S			S	S				S	S	S		
P. ?restrictum		S												S		S		
Hygrophorus conicus		G	G	G	G		G	G		G		G	G		G	G		
Xeromphalina pubescentipes	W				W					W		W	W	W	W	W	W	
Mycena leptocephala	G							G	G	G	G		G	G	G	G	G	
Puccinia crandallii	P	P	P		P		P	P		P			P		P		P	
Lycoperdon umbrinum	G		G			G							G				G	
Galerina 20789	G	G	G	G	G				G	G		G	G		G	G	G	
Rhodophyllus 22089B		G															G	
Puccinia coronata		P	P		P			P	P						P		P	
Tricholoma sp.			G	G					G					G		G	G	
Phragmidium montivagum			P		P	P				P	P	P			P	P	P	
Mycena plumbea	G		G	G	G	G		G	G	G	G		G	G			G	
Mycena plumbea f. *robusta*	G	G	G	G	G	G	G	G		G		G					G	G
M. stannea	G			G				G	G		G	G			G	G		G
Collybia sp.	G									G	G			G	G	G	G	G
Clitocybe sp.	G	G	G	G					G	G	G	G		G	G	G	G	G
Collybia dryophila	G		G		G					G				G	G	G		G
Mycena delicatella	G				G								G	G	G	G	G	G
Penicillium raciborskii	S	S	S	S		S	S						S					S
Mycena spp.	G	G	G	G	G		G	G	G	G	G		G	G	G	G	G	G
Agaric spp.	G	G		G	G	G		G	G	G	G	G	G	G	G	G	G	G
Brown spored agarics spp.	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G
Aspergillus niger		S				S						S	S				S	S
Lycoperdon gemnatum		G						G	G	G		G	G	G	G	G	G	G
Mycena pura		G	G				G	G	G	G	G	G	G	G	G	G	G	G
Hygrophorus miniatus			G															G
Cortinarius spp.			G			G		G	G	G	G	G	G	G	G	G	G	G
Spicaria violacea				S														
Collybia 19822				G														
Clitocybe 22525				G														
Cortinarius 21742				G														
Pink Agaric 21738				G														
Propolis faginea				W														
Lachnum leucophaeum				L														
Galerina 19673				G														
G. camerina					G													
Collybia ?oyes					G													
Tricholoma cinerascens					G													

TABLE 4A. Continued

Species / Association	F			S			Pa			Ps			D			G		
Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Lepiota 21219					G													
Pink Agaric 21197					G													
Pink Agaric 22722					G													
Pink Agaric 22723					G													
Mycena olivaceobrunnea					G													
Rhodophyllus 21827					G													
Rhodophyllus 21839					G													
Clitocybe 22730					G													
Taphrina potentillae					P													
T. confusa					P													
Marssonina potentillae					P													
Ascochyta lomatiae					P													
Entyloma compositarum					P													
Gloeosporium wyethiae					P													
Mucilago spongiosa					T													
Penicillium viridicatum					S													
Thielavia sepedonium					SC													
Mycena tenella						G												
M. pectinata						G												
Lyophyllum sp.						G												
Bovista pila						G												
Tricholoma 22216						G												
Pink Agaric 22227						G												
Collybia 22217						G												
Psathyrella limiccla						G												
Mollisia carduorum						L												
M. ?stictella						L												
Physarum bivalve						L												
Helotium sp.						L												
Helotium sp.						L												
Pyrenomycete						L												
Cyphella sp.						L												
Tubercularia sp.						L												
Papulospora sp.						S												
Vermicularia lileacearum						T												
Didymellina iridis						T												
Heterosporium gracile						T												
Ramularia arvensis						P												
Conocybe 21745				W	W													
Hapalopilus rutilans				W	W													
Cyphella capula				L		L												
Mycena capillaris				G		G												
Dark spored agaric					G	G												
Puccinia leveillei					P	P												
Pythium debaryanum					S		S											
Psathyrella agrariella					G			G										
Clitocybe 21185						G		G										
Pink agaric						G		G										
Coprinus ephemereus				G		G			G									
Microsporum gypseum					SC	SC			SC									
Phragmidium speciosum				P		P				P								
Corticium udiccla				W	W	W				W								
Tricholoma personatum					G	G				G								
Stereum patelliforme				W						W	W							
Tubaria 24537				W	W						W							
Galerina 19543				G		G					G							
Lyophyllum 21487				G							G							
Tubaria sp.				G							G							
Stropharia sp.						G			G		G							
Tubaria pellucida				W						W		W						

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Mycena parabolica					G								G					
M. albidula					G								G					
Collybia 21835					G								G					
Mycena cinerella					G	G							G					
Pink agaric 21749				G	G	G								G				
Tubaria 20855				W	W	W					W			W				
Galerina 19674				G							G			G				
Lepiota 21730				G	G	G								G				
Tricholoma 21165						G								G				
Crepidotus ?submollis				W					G						W			
C. sphaerosporus				W										W	W			
Lentinus omphalodes				W											W			
Psathyrella atrifolia				G										G	S			
Penicillium decumbens				S	S			S		S					G			
Galerina vittaeformis					G				G						S			
Lepiota 20713					G	G	G		G		P			G	G			
Dibotryon morbosum					P										P			
Septoria symphoricarpi					P	P									P			
Asteroma tenerrimum v. *erythronii*					P							P			P			
Puccinia balsamorhizae						P			P						P			
Hygrophorus 21447				G						G						G		
Clitocybe 21109				G		G		G			G	G		G		G		
Tricholoma 20760				G	G					G				G	G	G		
Coleosporium solidaginis					P											P		
Clitocybe 22478					G											G		
Galerina sp.				G	G		G	G	G	G	G	G		G	G	G	G	
Cystoderma granulosa				G			G	G	G	G	G	G	G	G	G	G	G	
Helotium virgultorum				L	L	L				G	L	L	L	L		L	L	
Clitocybe 20905					G				G	L	G	L	G	G			G	
Hormodendrum viride						S				G	G	G	G				S	
Fusarium sp.						S									S			
Cortinarius 20765						G	G				G	G			G	G	G	
Crepidotus variabilis				W														W
Mycena filopes				G	G						G				W			G
Clitocybe concava				G											G			G
Tricholoma terreum				G			G	G	G	G	G		G	G	G	G	G	G
Cortinarius 19810A				G				G		G				G			G	G
Stereum hirsutum				W											W			W
Corticium spp.				W		W	W		W	W		W		W		W		W
Lophodermellina hysterioides					PL							PL						PL
Galerina 19577					G		G			G	G		G	G	G	G	G	G
Geastrum rufescens						G							G					G
Pleurotus sp.							G											
Cortinarius 22645							G											
Tricholoma 22635							G											
Omphalina 21642							G											
Clavariadelphus maricola							G											
Dasyscypha subtilissima							L											
Coniophora sp.							W											
Mollisia sp.							W											
Arcyria pomiformis							W											
Arcyria incarnata							W											
Enerthenema melanosporum							W											
Merulius fugax							W											
Tomentella fusca							W											
Puccinia atrofusca							P											
Hypomyces chrysospermus							F											
Exosporium pedunculatum							W											
Penicillium frequentens							S											
Mortierella sp.							S											
Conocybe tenera								G										
Tricholoma 19601								G										
Tricholoma 21977								G										
Tricholoma 22848								G										
Cortinarius 22825								G										

TABLE 4A. Continued

Species \ Association	F			S			Pa			Ps			D			G		
Species \ Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Cortinarius 21762								G										
Rhodophyllus 19602								G										
Rhodophyllus 21992								G										
Coprinus plicatilis								G										
Calvatia craniiformis								G										
Galerina 21993								G										
Clitocybe 22004								G										
Clitocybe 22826								G										
Clitocybe 23424								G										
Psathyrella kanousii								G										
Albugo tragopogonis								P										
Aspergillus fumigatus								S										
Hygrophorus albidus									G									
H. pusillus									G									
Mycena abramsii									G									
Clitocybe 19528									G									
Saccobolus violaceus									D									
Coprinus cordisporus									D									
Psathyrella pratensis									G									
Amanitopsis vaginata var.									G									
Pholiota 22240									G									
Stropharia semiglobata v. *typica*									D									
Lepiota 21356A									G									
Lepiota 21364									G									
Inocybe fastigiata v. *curreyi*									G									
Inocybe 22249									G									
Pink agaric 22261									G									
Pink agaric 21780									G									
Lyophyllum 22278									G									
Galerina rubiginosa									G									
Cyathus stercoreus									D									
Fomes officinalis									T									
Oidium sp.									W									
Corticium subsimile									W									
Peniophora cinerea									W									
Gymnosporangium bethelii									P									
Ovularia pusilla									P									
Septoria rhoina									P									
Penicillium piscarium									S									
Cunninghamella echinata									S									
Omphalina 19578							G	G										
Collybia plexipes							G	G										
Inocybe fastigiata v. *?arenicola*							G		G									
Puccinia rubigo-vera v. *apocrypta*							P		P									
Hygrophorus 21630							G	G		G								
Peniophora cremea							W		W	W								
Pink agaric 20911							G			G	G							
Mycena pseudotenax							G			G	G							
Penicillium nigricans							S		S		S							
Cortinarius 21756								G			G							
Clitocybe 20975								G			G							
Ascobolus stercorarius									D		D							
Patella theleboloides									D		D							
Collybia 20991									G		G							
Stemonitis favogenita									W		W							
Inocybe friesii f. *nemorosa*									G		G							
Lycoperdon rimulatum									G				G					
Inocybe radiata									G		G							
Pellicularia subcoronata							W			W		W	W	W				
Cortinarius 22003							G	G						G				

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Cryptoporus volvatus							W	W				W		W				
Psathyrella candolleana									G					G				
Mycena pseudoclavicularis							G		G						G			
M. fragillima									G	G					G			
Odontia crustosa									W					W	W			
Inocybe 21639							G									G		
Hydnangium sp.							H									H		
Peniophora gracillima							W		W						W	W		
Tyromyces caesius							W						W	W	W	W		
Propolis leonis							T	T	T					T	T	T		
Lophodermium pinicolum							PL	PL		PL	PL				PL	PL		
Cortinarius 22505								G								G		
Dacrymyces abietinus								W		W	W			W	W	W		
Lyophyllum 21487								G						G		G		
Calocera cornea									W						W	W		
Collybia racemosa									G	G			G			G		
Mycena plicosa									G				G	G	G	G		
Clitocybe 24585									G				G		G	G		
Cystoderma cinnabarina									G						G	G		
Thelephora caryophyllea							G			G				G		G	G	
Dacrymyces deliquescens							W	W			W		W	W	W		W	
D. punctiformis							W		W					W	W	W	W	
Suillus punctipes							GM	GM	GM		GM	GM	GM	GM	GM	GM	GM	
Mycena elegantula							W			W		W	W	W	W	W	W	
M. metata							G	G	G	G	G	G	G	G	G	G	G	
Cortinarius 20816							G	G		G			G			G	G	
Cortinarius 21348							G					G	G		G		G	
Cystoderma fallax							G	G		G	G	G	G	G		G	G	
Tricholoma 19648							G									G	G	
Hygrophorus eburneus							G	G		G	G	G				G	G	
H. pratensis							G	G		G	G	G					G	
Clitocybe peltigerina							?P		?P	?P			?P			?P	?P	
Clitocybe 21079							G										G	
Cumminsiella mirabilissima								P		P	P				P	P	P	
Galerina 19806								G			G	G		G	G	G	G	
Clavarielia abietina								L		L	L		L	L		L	L	
Agaricus diminutivus									G					G			G	
Polyporus spp.									W						W	W	W	
Stereum sanguinolentum									W				W	W	W	W	W	
Marasmius androsaceus							L			L	L	L	L	L	L	L	L	L
M. fuscopurpureus							G	G		G	G		G	G	G	G	G	G
Mycena purpureofusca							W	W	W	W	W		W	W	W	W	W	W
Collybia albipilata							C	C		C	C	C	C	C	C	C	C	C
Tricholoma 24371							G									G		G
Hygrophorus chrysodon							G	G	G	G		G		G	G	G	G	G
Hebeloma crustuliniforme							G	G		G	G	G	G	G		G	G	G
Poria spp.							W		W		W			W	W	W	W	W
Hirschioporus abietinus							W		W	W	W	W	W	W	W	W	W	W
Ceratiomyxa fruticulosa							W				W				W			W
Coltricia perennis							G		G							G	G	G
Inocybe (indet.)							G			G	G	G		G	G	G	G	G
Haplographium biocolor							S			S								S
Armillaria mellea								?P						?P		?P	?P	?P
Auriscalpium vulgare							C	C	C	C	C	C	C	C	C		C	C
Cortinarius 19599								G		G			G	G		G	G	G
Mycena amabilissima								G		G	G		G	G	G		G	G
M. subplicosa								G	G	G	G		G	G	G	G	G	G
M. epipterygioides								G		G	G	G	G	G	G	G	G	G
Russula borealis									G					G	G	G	G	G
Leucopaxillus amarus f. *bicolor*									G	G	G		G	G		G		G

TABLE 4A. Continued

Species / Association	F			S			Pa			Ps			D			G		
Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Mycena citrinomarginata									G	G	G		G	G	G			G
M. constans									G						G			G
Dacrymyces palmatus									W		W		W		W	W	W	W
Peniophora sp.									W	W	W			W				W
Penicillium kapuscinskii									S	S	S	S	S	S	S		S	S
Hygrophorus spp.									G		G		G			G	G	G
Collybia fulvipes									G		G	G	G	G	G	G	G	G
Clavaria sp.									G	G				G		G	G	G
Lepiota clypeolaria									G			G		G		G	G	G
Collybia cirrhata										G								
Collybia 20884										G								
Clavariella pinicola										G								
Collybia tuberosa										G								
Collybia 22579										G								
Clitocybe serrusata v. *pithyophila*										G								
Clitocybe 22607										G								
Clitocybe 24390										G								
Cortinarius 21605										G								
Cortinarius 20722										G								
Cortinarius 21561										G								
Marasmius 20875										G								
Marasmius rotula										L								
Omphalina 19753										G								
Inocybe geophylla var. 21589										G								
Inocybe posterula										G								
Lepiota 21952										G								
Pleurotus 21610										G								
Tricholoma 21512										G								
Hygrophorus 22615										G								
Lachnum virginellum										L								
Helotium cyathoideum										L								
Thelephora intybacea										W								
Trichoscyphella tenuipilosa										?P								
Diderma sp.										W								
Solenia ochracea										W								
Mucronella aggregata										W								
Tulasnella violea										W								
Taphrina aurea										P								
Melampsora occidentalis										P								
Microsphaera alni										P								
M. symphoricarpi										P								
Scopulariopsis brevicaulis										S								
Mucor janus										S								
Penicillium diversum v. *aureum*										S								
Coprinus narcoticus												D						
Conocybe spicula f. *spicula*											G							
Galerina hypnorum ss. Kühner											G							
Coprinus niveus											G							
Clitocybe 20992											G							
Clitcybe 22661											G							
Ripartites tricholoma											G							
Leucopaxillus giganteus											G							
Mycena lilacifolia											W							
M. blumanea											G							
M. subvitrea											G							
Psilocybe subviscida											G							
Panaeolus foensicii											D							
Stropharia semiglobata v. *stercoraria*											D							
Psathyrella obtusata											D							
Flammula nr. *spumosa*											G							

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Pink agaric 20973											G							
Pink agaric 21197											G							
Pink agaric 22684											G							
Leptotus sp.											L							
Flammula 24873											G							
Lepicta 21767											G							
Lepicta 21695											G							
Rhodophyllus 21974											G							
Cortinarius 22682											G							
Cortinarius 21768											G							
Inocybe deglubens											G							
Helotium lutescens											L							
Trichia favoginea											W							
Rutstroemia sp.											L							
Stereum fasciatum											W							
Penicphora affinis											W							
Ceratiomyza fruticulosa v. *poroides*											W							
Serpula americana											W							
Peniophora mollis											W							
Coniophora arida											W							
Trichia sp.											W							
Helotium sp.											L							
Papularia sphaerosperma											S							
Russula 20841												G						
Hygrophorus gliocyclus												G						
Cortinarius 22125												G						
Cortinarius 22174												G						
Cortinarius 22173												G						
Clitocybe 20672												G						
Naucoria sp.												G						
Inocybe fastigiata var. 22183												G						
Pleurotus 22160												G						
Penicillium (*brevi-compactum* Ser.)												S						
P. raistrickii												S						
P. nr. *rugulosum*												S						
Mortierella pusilla												S						
Pythium rostratum												S						
Clitocybe 22661										G	G							
Collybia 22150											G	G						
Clitocybe 22441										G			G					
Kuehneromyces 24734										G			G					
Puccinia rubigo-vera										P			P					
Pythium vexans											S		S					
Cortinarius 21810											G		G					
Inocybe fastigiata var. 21948												G		G				
Inocybe 22148												G		G				
Clitocybe 19861											G		G					
Helvella infula											G			G				
Phlebia albida											W			W				
Collybia cookei										G					G			
Helvella elastica										G					G			
Pellicularia vaga										W					W			
Mycogone rosea										F					F			
Fomes annosus										T					T			
Gloeoporus dichrous										W				W	W			
Pluteus cervinus										W	W			W	W			
Clitocybe ditapoda											G				G			
Leptotus retirugis											M				M			
Clavariadelphus truncatus										G						G		
Clitocybe 20786										G	G			G		G		

TABLE 4A. Continued

Species	Association	F			S			Pa			Ps			D			G		
	Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Clitocybe 20912											G		G	G	G	G	G		
Clitocybe 24547											G						G		
Cortinarius 21543											G						G		
Inocybe agglutinata											G		G				G		
I. trechispora											G		G				G		
Cortinarius 20757											G						G		
Cortinarius 20716											G		G				G		
Galera sp.											G						G		
Inocybe geophylla v. *geophylla*											G		G		G		G		
I. friesii f. *laricina*											G					G	G		
Otidea onotica											G					G	G		
Tyromyces fragilis												W			W	W	W		
Exidia saccharina												W				W	W		
Russula 20842													G				G		
Tricholoma imbricatum													G				G		
Gomphidius rutilans													G				G		
Tyromyces anceps													W				W		
Clavariella subdecurrens											G		G	G			G	G	
Otidea concinna											G		G	G	G	G	G	G	
Mycena rosella											G		G	G	G	G	G	G	
Clitocybe 21109											G			G				G	
Cortinarius 21572											G							G	
Cortinarius 20752											G		G				G	G	
Cortinarius 20818											G				G		G	G	
Cortinarius 21593											G	G	G		G		G	G	
Cortinarius 20729											G						G	G	
Thelephora terrestris											L			L				L	
Gloeophyllum sepiarium											W					W	W	W	
Cronartium coleosporioides											P							P	
Collybia conigena												C		C				C	
Clitocybe 21065												G	G			G		G	
Hygrophoropsis aurantiacus												G	G				G	G	
Cantharellus cibarius												G						G	
Pholiota 21037												G						G	
Lycogala epidendrum												W				W		W	
Phaeolus schweinitzii													T		T			T	
Mycena flavoalba													G					G	
Pholiota 22186													G					G	
Naematoloma capnoides													W					W	
Flammula 22069													G					G	
Clavariadelphus ligulus											G			G			G		G
Helvella lacunosa											G					G			G
Cortinarius 21445											G				G		G	G	G
Cortinarius 20718											G		G		G		G	G	G
Cortinarius 19572											G			G	G	G	G	G	G
Inocybe geophylla var. *lateritia*											G		G		G		G		G
Onnia tomentosa											G								G
Russula delica											G			G			G		G
Russula 21526											G		G				G	G	G
Russula sp.											G			G	G	G	G	G	G
Inocybe geophylla v. *lilacina*											G						G		G
Tremella mesenterica											W								W
Hymenochaete tabacina											W		W	W	W	W	W	W	W
Mycena atroalboides												G		G		G	G	G	G
Guepiniopsis torta												W			W	W			W
Mycena capillaripes												G			G				G
Lactarius sanguifluus												G			G	G	G		G
Cortinarius 20780													G				G		G
Cortinarius 19810B													G				G		G
Clitocybe 22151													G						G

TABLE 4A. Continued

Species / Association	F			S			Pa			Ps			D			G		
Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Flammula 22059												G			G	G	G	G
Trametes carbonaria												W				W		W
Absidia glauca												S						S
Inocybe subdestricta												G		G			G	G
Scleroderma cepa													G					
Mycena gracilis													G					
Mycena subcana													G					
Cortinarius 20955													G					
Pink agaric 19570													G					
Pink agaric 21669													G					
Amanita muscaria													G					
Hebeloma mesophaeum													G					
Otidea alutacea f. *alutacea*													G					
Morchella angusticeps													G					
Hysterangium ?darkeri													H					
Discina ancilis													G					
Morchella esculenta													G					
Panaeolus coprophilus													D					
Otidea alutacea f. *microspora*													G					
Tubaria ferruginea													G					
Clitocybe 22441A													G					
Tricholoma 22429													G					
Marasmius 22411													G					
Tricholoma 24352													G					
Hymenochaete cinnamomeus													W					
Arcyria nutans													W					
Inocybe nr. *rubens*													G					
Cladosporium epimyces													F					
Phyllosticta cylindrica													P					
Coprinus radians													G	G				
Cortinarius 21091														G				
Cortinarius 22779														G				
Mycena leptocephala f. *ammoniaca*														G				
Clitocybe 21098														G				
Clitocybe 21941														G				
Clitocybe 21908														G				
Clavariadelphus unicolor														G				
Lepiota 21952														G				
Lepiota 21099														G				
Otidea leporina v. *minor*														G				
Lepiota 21125														G				
Lepiota 21869														G				
Lepiota 21863														G				
Rhodophyllus 21974														G				
Rhodophyllus 24428														G				
Rhodophyllus 21133														G				
Pink agaric 22790														G				
Crepidotus nephrodes														W				
C. crocophyllus														W				
Agaricus silvicola														G				
Flammula 21932														G				
Tricholoma 22798														G				
Tricholoma 21853														G				
Tricholoma 22774														G				
Tricholoma 21844														G				
Tricholoma 22821														G				
Lyophyllum 22786														G				
Lyophyllum 21892														G				
Lyophyllum 20788														G				
Inocybe eutheles														G				

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Inocybe geophylla v. *violacea*														G				
Inocybe obscura var. 24459														G				
Hygrophorus agathosmus														G				
Russula 21928														G				
Lactarius 21919														G				
Collybia 22755														G				
Nectria cinnabarina														P				
Poria carbonica														W				
Didymium minus														W				
Dacrymyces ellisii														W				
Hypocrea sp.														W				
Corticium polygonium														W				
Brachysporium obovatum														W				
Lachnum virgineum														W				
Penicillium canescens														S				
Macrosporium commune														S				
Hysterographium fraxini														W				
Phyllosticta sp.														P				
Cronartium ribicola														P				
Sphaerotheca pannosa														P				
Puccinia pimpinellae														P				
Gomphidius roseus v. *homeobasis*														G				
Lentinus sp.															W			
Galerina hypnorum ss. Atk.															G			
G. semilanata															G			
Marasmius 21340															G			
Clitocybe rivulosa															G			
C. cyathiformis															G			
Mycena pusilla															G			
Trichloma 19648															G			
Peziza sp.															G			
Coprinus 21324															G			
Lepiota 21318															G			
Lepiota 21315															G			
Lepiota 21869															G			
Inocybe 25166															G			
Inocybe nr. *bakeri*															G			
I. obscura var. 18963															G			
Agaricus hondensis															G			
Collybia 20991															G			
Collybia 21331															G			
Tremella mesenterica															W			
Lachnum sp.															L			
Physarum cinereum															W			
Coriolus versicolor															W			
Poria versipora															W			
Coriolus hirsutus															W			
Tomentella sp.															W			
T. fusca															W			
Peniophora amoena															W			
Helminthosporium ochroleucum															W			
Mucor geophilus															S			
Peronospora claytoniae															P			
Dinemasporium graminicolum															L			
Ramularia smilacinae															P			
R. philadelphi															P			
R. pentstemonis															P			
Phyllosticta vagans															P			
Hyalopsora polypodii															P			
Cytospora globulifera															P			
Dasyscypha patula															L			

TABLE 4A. Continued

Species / Association	F			S			Pa			Ps			D			G		
Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Cytospora globulifera													G	G	P			
Clavaria acris													G	G				
Tricholoma 23432													G	G				
Fomes subroseus													WT	WT	WT			
Psathyrella solheimii														G	G			
Lepiota 21319														G	G			
Xylaria digitata														W	W			
Aleurodiscus sp.														W	W			
Panellus mitis													W	W		W		
Gomphidius subroseus													G	G		G		
Clitocybe 22288													G		G	G		
Stromatocrea cerebriformis														W		W		
Pholiota erinacea														W		W		
Inocybe olympiana														G		G		
Cortinarius 21470														G		G		
Mycena piceicola															G	G		
Cortinarius 21551															G	G		
Cortinarius 20712															G	G		
Pellicularia sp.															W	W		
Poria lenis															W	W		
Otidea leporina v. *leporina*													G	G	G	G	G	
Marasmius piceinus													L	L		L	L	
Cortinarius 19569													G			G	G	
Pseudoplectania nigrella													G			G	G	
Peniophora luna													W				W	
P. sanguinea													W	W			W	
Porodaedalea pini													WT				WT	
Gomphidius oregonensis													G	G			G	G
Mycena vulgaris														G		G	G	
Pholiota 21076														G			G	
Tricholoma 21129														G			G	
Tricholoma 20751														G			G	
Inocybe pallidipes														G		G		G
Pleurotus candidissimus														W		W	W	
Phlogiotis helvelloides														G	G		G	
Leocarpus fragilis														WL	WL		WL	
Helotium caudatum															L		L	
Clitocybe 23557															G		G	
Boletinus amabilis-lakei													GM	GM	GM	GM		GM
Geastrum fornicatum													G	G			G	G
Mitrula abietis													L	L	L	L	L	L
Laccaria laccata													G			G	G	G
Hygrophorus paludosus													G	G	G	G	G	G
H. inocybeformis f.													G					G
Clitocybe 22356													G					G
Dasyscypha ciliata													L	L			L	L
Crucibulum levis													W				W	W
Helotium citrinum													W	W		W		W
Gomphidius glutinosus													G					G
Pseudohydnum gelatinosum														W	W		W	W
Polyporus elegans														W		W	W	W
Mycena adonis														G	G			G
Clitocybe 24442														G				G
Suillus subluteus														GM		GM	GM	GM
Spathularia flavida														L		L	L	L
Russula 20842														G		G	G	G
Fomes pinicola														WT	WT	WT	WT	WT
Helminthosporium pseudotsugae														T	T	T	T	T
Galerina badipes															G			G

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Marasmius perforans															L	L		L
Mycena fusipes															G		G	G
Cortinarius 21800															G		G	G
Russula 20840															G	G		G
Russula 20839															G	G	G	G
Reticularia lycoperdon															W			W
Humarina semiimmersa																G		
Paxillus panuoides																W		
Polyporus picipes																W		
Dentinum repandum																G		
Phylloporus rhodoxanthus ssp. *americanus*																G		
Clitocybe 19853																G		
Clitocybe 19528																G		
Clitocybe 22525																G		
Clitocybe 24584																G		
Cortinarius 20761																G		
Cortinarius 21549																G		
Cortinarius 20814																G		
Cortinarius 20810																G		
Cortinarius 21516																G		
Cortinarius 21547																G		
Cortinarius 21473																G		
Cortinarius 22504																G		
Cortinarius 19855																G		
Cortinarius 20725																G		
Cortinarius 20757																G		
Armillaria 19856																G		
Lepicta 20713																G		
Flammula 24745																W		
Flammula sp.																W		
Tricholoma 20759																G		
Tricholoma 21496																G		
Tricholoma 21512																G		
Tricholoma 24352																G		
Omphalina 20787																G		
Omphalina 22562																G		
Rhodophyllus 20773																G		
Pink Agaric 20801																G		
Lyophyllum 21495																G		
Lyophyllum 20779																G		
Lyophyllum 20788																G		
Pholiota 22186																G		
Hygrophorus 22647																G		
Inocybe geophylla v. *lateritia* f. *perplexans*																		
I. kauffmanii																G		
Suillus subtomentosus																GM		
Collybia 21451																G		
Collybia 21466																G		
Collybia 21494																G		
Russula 20844																G		
Russula 22507																G		
Cortinarius 21459																G		
Clavariadelphus pistillaris																G		
Donkella corniculata																G		
Clavaria fusiformis																G		
Hymenogaster ?remyi																H		
Aleurodiscus amorphus																T		
Grandinia farinacea																W		
Corticium sp.																W		
C. furfuraceum																W		

TABLE 4A. Continued

Species / Association	F			S			Pa			Ps			D			G		
Plot	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Penicphora hastata																W		
Odontia fimbriata																W		
Exidia spiculosa																W		
Physarum ?rubiginosum																W		
Vararia granulosa																W		
Melampsora arctica																P		
Rhytisma salicinum																P		
Coleroa dickei																P		
Russula delica																	G	
Clitocybe candicans																	G	
Clitocybe 20975																	G	
Tricholoma 21165																	G	
Tricholoma 22774																	G	
Cortinarius 22075																	G	
Cortinarius 21036																	G	
Cortinarius 22067																	G	
Calocera viscosa																	G	
Onygena corvina																	D	
Pholiota 21061																	G	
Inocybe subochracea																	G	
Inocybe castanea																	G	
Inocybe nr. *lanuginosa*																	G	
Flammula 22025																	G	
Clitocybe 21112																	G	
Rhodophyllus 22089A																	G	
Microglossum fumosum																	G	
Lachnum leucophaeum																	L	
Phlebiella candidissima																	W	
Sebacina sp.																	W	
Poria subacida																	W	
Corticium bicolor																	W	
Tyromyces undosus																	W	
Trametes americana																	W	
Uromyces heterodermus																	P	
Monosporium agaricinum																	F	
Septoria coptidis																	P	
Pucciniastrum myrtillis																	P	
Cortinarius 19598																		G
Amanitopsis vaginata var.																		G
Xeromphalina campanella																		W
Cortinarius 19622																		G
Hygrophorus virgineus																		G
H. parvulus																		G
Marasmius 19744																		G
M. chordalis																		G
Tricholoma chrysites																		G
Russula albidula																		G
R. palustris																		G
Clitocybe clavipes																		G
Lyophyllum sp.																		G
Mycena oregonensis																		G
M. flavoalba v. *microspora*																		G
M. maculata																		G
M. subaquosa																		G
M. aurantiidisca																		G
Omphalina 19753																		G
Coriolus pargamenus																		W
Daedaleopsis confragosa																		W
Poria sp.																		W
P. ferrea																		W

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Sordaria bombardioides																		D
Poria bombycina																		W
Merulius tremellosus																		W
Corticium livido-caeruleum																		W
Odontia bicolor																		W
O. arguta																		W
Excidia recisa																		W
Peniophora carnosa																		W
Chlorociboria aeruginosa																		W
Fuligo septica																		W
Kuehneromyces cookii																		W
Helotium sp.																		L
Hypomyces lactifluorum																		F
H. aurantius																		F
Uredinopsis macrospora																		P
Septoria rubi																		P
Penicillium fuscum																		S
Stachylidium extorre																		S
Gomphidius smithii																		G
Inocybe albodisca																		G
I. nr. *langei* v. *maicr*																		G
I. geophylla v. *geophylla*																		G
I. pallidobrunnea																		G
Hygrophorus speciosus																GM	GM	
Kuehneromyces sp.																W	W	
Pholiota adiposa																WT	WT	
Boletinus cavipes																GM	GM	
Suillus grevillei																GM	GM	
Cyphella alboviolascens																W	W	
Tomentella echinospora																W	W	
Peniophora tenuis																W	W	
Cortinarius 20811																G		G
Cortinarius 19621																G		G
Russula 21266																G		G
Peltigera canina v. *spongiosa* Tuck.			G		G													
P. membranacea (Ach.) Nyl.			G												GR			
P. scutata (Dicks.) Duby			G												D			
Cladonia chlorophaea f. *simplex* (Hoffm.) Arn.			G				G						G		GR			
Diploschistes actinostromus (Pers.) Zahlbr.		G							R									
Peltigera canina v. *rufescens* (Weis.) Mudd	G	G	G				G			G		G	G		GR		G	
Cladonia chlorophaea (Flk.) Spreng.	G												G		C		G	
C. fimbriata (L.) Fr.	G	G					G	G	GWC	GW		W	GR	W	RC		G	W
C. pyxidata (L.) Hoffm.		G						RG										
Physcia grisea (Lam.) Zahlbr.		G		D														
Xanthoria polycarpa (Ehrh.) Bicbr.				D							C	D			C			
Parmelia olivacea Nyl.					D													
P. elegantula					D									DC				
Candelaria concolor (Dicks.) Arn.					D					D		D						
Rinodina finkii Magn.						D						D						
Alectoria fremontii ssp. *erikssonii* D. R.							C											
Diploschistes scruposus (L.) Norm.								R										
Lecanora rubina (Vill.) Ach.								R										
L. cinerea (L.) Roehl.								R										

TABLE 4A. Continued

Species / Association / Plot	F N	F C	F S	S N	S C	S S	Pa N	Pa C	Pa S	Ps N	Ps C	Ps S	D N	D C	D S	G N	G C	G S
Lecidea atrobrunnea (Ram.) Schaer.								R										
Umbilicaria decussata (Vill.) Zahlbr.								R										
U. hyperborea Ach.								R										
Cladonia nemozyna (Ach.) Nyl.								C										
Alectoria jubata (L.) Ach.									C									
Lecidea parasaema Ach.									C									
Buellia badia (E. Fr.) Mass.									R									
Umbilicaria phaea Tuck.									R									
Parmelia sorediata (Ach.) Roehl.									R									
Rhizocarpon bisporum Magn.									R									
Usnea dasypoga (Ach.) Roehl. Em. Mot.									C									
Parmelia conspersa (Ehrh.) Ach.									R									
Cladonia multiformis f. *subascypha* (Vainio) Evans									G									
C. pyxidata (L.) Hoffm.									W									
C. cornutoradiata (Coem.) Sanst.									G				.					
Lecidea rubiformis Wahl.									R									
L. cyanea (Ach.) Roehl.									R									
L. columbiana H. Magn.									R									
L. fuscoatra (L.) Ach.									R									
Peltigera canina v. *ulorrhiza* (Flk.) Schaer.									G									
Rhizocarpon geographicum (L.) DC.								R	R									
R. eupatraeum (Nyl.) Arn.								R	R									
Lecidea cascadensis Magn.								R	R									
Crocynia lanuginosa (Ach.) Hue.								R		D								
Cladonia ochrochlora									C				G					W
Centraria californica Tuck.							C				C	C						
Parmelia fuliginosa (Fr.) Nyl.								C				CD						
Buellia punctata (Hoffm.) Magn.								C				D						
Cladonia cariosa (Ach.) Spreng.							G						D					
Parmeliopsis ambigua (Wulf.) Nyl.									C			W	C					
Cladonia major (Hag.) Sandst.							G								R			
C. glauca Flderke							G								R			
Parmelia saxatilis (L.) Ach.								R							R			
Lecanora rupicola (L.) Zahlbr.								R	R						R			
Lecidea subfusca Nyl.									R						C			
Usnea laricina Vainio									C						C			
Rhizocarpon grande (Flk.) Arn.									R						R			
Leptogium lichenoides (L.) Zahlbr.									RM						RM			
Cetraria platyphylla (Tuck.) Herre							C	C			C	C	C	C		C	C	
C. juniperina (L.) Ach.							C			C			C		C	C	C	
Alectoria jubata v. *lanestris* Ach. Em. DR.							C	C	C	C			C		C	C	C	
Letharia vulpina (L.) Vainio							C	C	C	C	C	C	C	C	C	C	C	
Cetraria chlorophylla (Willd.) Vainio									C	C	C		C	C		C	C	
Parmelia physodes (L.) Ach.									C				C	C		C	C	
Cladonia scabriuscula f. *surrecta* (Flk.) Sandst.							G	G	R				G		RG		W	G
Parmelia enteromorpha Ach.							C		C	C	C	C	C	C	C	C	C	C
Cetraria glauca (L.) Ach.							C	C		C	C	C	C	C		C	C	C
Lecanora subrugosa Nyl.										D								
Lecidea varians Ach.										C								
L. olivacea (Hoffm.) Mass.										D								

TABLE 4A. Continued

Species / Association / Plot	F N	F C	F S	S N	S C	S S	Pa N	Pa C	Pa S	Ps N	Ps C	Ps S	D N	D C	D S	G N	G C	G S
Physcia tenella (Scop.) Nyl.										D								
Lecidea scalaris Ach.										C								
L. viridescens (Schrad.) Ach.												W						
Bacidia chlorococca (Graewe) Lettau												C						
Cladonia major f. *denticulata* Flk.												W						
C. cariosa f. *cribrosa* (Wallr.) Vainio												G						
C. borbonica f. *cylindrica* Evans												GW						
C. gracilis (L.) Willd.												W						
Lecanora symmicta Ach.												W						
L. distans (Pers.) Nyl.												D						
Candelariella cerinella (Flk.) Zahlbr.												D						
Candelaria concolor v. *effusa* (Tuck.) Merr. & Burnh.												D						
Parmelia subaurifera Nyl.												D						
Alectoria nidulifera Norrl.												C						
Caloplaca oregona Magn.												D						
Rinodina coloradina Magn.												D						
Xanthoria candelaria (Ach.) Arn.												D						
Rinodina hallii Tuck.												D						
Peltigera degeni Geyel.												GW						
Parmelia fuliginosa v. *laetevirens* Flot. ex Nyl.												DC		D				
P. sulcata v. *sulcata* f. *eusulcata* Maas. G.												D		D				
Xanthoria fallax (Hepp.) Arn.												D		D				
Parmelia aspera Mass.											C			C				
Physcia ascendens Bitt.												D		D				
Cladonia multiformis f. *simulata* Robbins										G					G			
Lecanora hageni Ach.												DC			C			
L. subfuscata Magn.												D			C			
L. varia (Hoffm.) Ach.												C		CD	C			
Cetraria stenophylla (Tuck.) Merrill											C		C			C		
Lecanora rugosa (Pers.) Nyl.										D							C	
Cladonia digitata (L.) Hoffm.										GW	G	W	G		GR		G	W
C. coniocrea (Flk.) Spreng.										GW		W				W		W
Parmelia tubulosa (Schaer.) Bitt.										C		C			C			
Peltigera canina v. *albescens* (Wahl.) Thoms.											G							G
Lecanora pacifica Tuck.												D		C				D
Parmelia sulcata Tayl.												CD		D		CR		D
P. exasperatula D. Not.												CD				C		
Cladonia chlorophaea f. *carpophora* (Flk.) Anders.													W		C			
Lecidea euphora (Flk.) Nyl.														CD				
Peltigera canina v. *rufescens* f. *innovans* (Korb.) Thoms.														G				
Parmelia fuliginosa v. *laetivirens* f. *eulaetevirens* Maas. G.														D				
Usnea glabrata (Ach.) Vainio														C				
Lecidea rugosella Magn.														D				
Rinodina nigra Fink															R			
Candelariella vitellina (Ehrh.) Müll. Arg.															R			
Physcia teretiuscula (Ach.) Lynge															R			
Lecanora muralis (Schreb.) Rabh.															R			
Buellia inquilina (Tuck.) Fink															D			
Nephroma helveticum Ach.															D			

TABLE 4A. Continued

Species / Association / Plot	F N	F C	F S	S N	S C	S S	Pa N	Pa C	Pa S	Ps N	Ps C	Ps S	D N	D C	D S	G N	G C	G S
Lecanora ?insignis Degel.															C			
Nephroma resupinatum (L.) Ach.															D			
Lecidea vernalis (L.) Ach.															C			
Rhizocarpon plenichrum (Tuck.) Merrill															C			
Cladonia coniocrea f. *ceratodes* (Flk.) Della Torre & Sarnth.															R			
C. crispita f. *divilsa* (Del.) Arn.															G			
C. multiformis f. *finkii* (Vainio) Evans															G			
C. squamosa (Scop.) Hoffm.															C			
Lecanora piniperda Koerb.															C			
Parmelia trichoptera Hue v. *trichoptera*															C			
P. saxatilis v. *saxatilis* f. *furfuracea* Schaer.															R			
Cetraria glauca f. *coralloidea* (Wallr.) Koerb.															C			
Evernia prunastri (L.) Ach.															C			
Xanthoria candelaria v. *leprosa* (Lamy.) Hillm.															R			
Buellia betulina (Hepp.) Th. Fr.															C			
Alectoria oregona Tuck.													C	C				
Peltigera aphthosa v. *variolosa* (Mass.) Thoms.													G		GR	G		
Alectoria jubata v. *impleza* (Hoffm.) Ach. Em. DR.														C		C		
A. jubata v. *prolixa* Ach. Em. Dr.														C		C		
Rinodina marysvillensis Magn.														D				D
Lobaria pulmonaria (L.) Hoffm.															R			G
Alectoria sarmentosa Ach.															C	C	C	C
Peltigera venosa (L.) Baumg.																G		
Cladonia cenotea (Ach.) Schaer.																W		
C. coniocrea f. *truncata* (Flk.) Della Torre & Sarnth.																	W	
C. chlorophaea f. *prolifera* (Wallr.) Arn.																	G	
C. ?turgida (Ehrh.) Hoffm.																	G	
Ochrolechia pallescens (L.) Mass.																	C	
Lecidea cinnabarina Fee.																	C	C
Cetraria atlantica (Tuck.) Dr.																		W
Lobaria oregona (Tuck.) Müll. Arg																		D
Lecidea tornoensis Nyl. & Saelan.																		C
Bacidia fuscorubella (Hoffm.) Bausch.																		D
Bilimbia sphaeroides (Dicks.) Koerb.																		D
Cladonia macilenta f. *styracella* (Ach.) Vainio																		W
C. multiformis Merrill																		W
Pertussaria arborea (Kreyer) Zahlbr.																		D
Lecanora pallida v. *cancriformis* (Hoffm.) Tuck.																		C
Cladonia bacillaris (Del.) Nyl.																		W
Encalyptra rhabdocarpa Schwaeg.	G																	
Riccia sorocarpa Bischoff.	G																	
Leptobryum pyriforme (Hedw.) Schp.			G															
Eurhynchium diversifolium (Schleich.) Br. & Sch.			G															
Funaria hygrometrica Hedw.			G															

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Pohlia cruda (Hedw.) Lindb.	G		G															
Ceratodon purpureus (Hedw.) Brid.	G		G	G	G	G	G		GR			GW						
Tortula ruralis (Hedw.) Crome		G	G			G						GW						
Bryum sp.			G			G				G	G	G						
Eurhynchium substrigosum Kindb.	G													W				
Tortula princeps De Not.	G			G				GR	GR	G	G		G		GR			
Brachythecium albicans (Hedw.) Schp.	G	G	G	G	G	G						GW	G	GB		G		
B. lutescens Hedw.			G									G		G				
Didymodon recurvirostris (Hedw.) Jenn.			G												R			
Bryum caespiticium Hedw.						G												
Claopodium crispifolium (Hook.) Ren. & Card.					G										GB			
Homalothecium nevadense (Lesq.) Ren. & Card.					B										R			
Campothecium amesiae Ren. & Card.									R									
Ptychomitrium gardneri Losq.									RG									
Rhodobryum roseum (Br. & Schp.) Limpr.									RG									
Rhacomitrium heterostichum v. *ramulosum* (Lindb.) Grout						G			G									
Grimmia alpestris (Web & Mohr.) Nees								R					R					
Polytrichum piliferum Hedw.								G							R			
Grimmia trichophylla Grev.								R		R			G		R			
Rhacomitrium heterostichum (Hedw.) Brev.									RG						G	G		
Polytrichum juniperinum Hedw.							G			GR		GW	G		G			GW
Barbula reflexa (Brid.) Brid.										G								
Brachythecium rivulare Br. & Schp.										G								
Hypnum subimponens Lesq.											G							
Tayloria serrata v. *tenuis* (Sm.) Bry. Eur.											G							
Onchophorus? sp.												G						
Grimmia trichophylla v. *muhlenbeckii* Huen.												W						
Dicranum scoparium Hedw. f.												G						
Brachythecium asperrimum (Mitt.) Sull.											G	W						
Brachythecium sp.										G					RB			
Orthotrichum affine Brid.												B		BG	B			
Cephalozziella papillosa Schiffner												GW			W			
Aulacomnium androgynum (Hedw.) Schwaegr.												GW			G	G		
Brachythecium glareosum (Bruch.) Br. & Sch.										G	G		G	W	G		G	
Timmia austriaca f. *brevifolia* (Ren. & Card.) Grout										R		GW	G			G	G	
Drepanocladus uncinatus (Hedw.) Warmst.												G					G	
Camptothecium megaptilum Sull.												GW			G		G	
Brachythecium rutabulum v. *flavescens* (Brid.) Br. & Schp.												G		G		G	G	
Eurhynchium oreganum (Sull.) Jaeg. & Sauerb.										G	G			BG	G		G	G
Rhytidiadelphus triquetrus (Hedw.) Warmst.										G	G	G	G	G	G	G		G
Orthotrichum speciosum Nees												G	G		R	G		W
Dicranum strictum Schleich.												GW	G	W	W	GW	GB	W
Atrichum undulatum (Hedw.) Pal. Beauv.													G					
Ceratodon purpureus f. *xanthopus* (Sull.) E. G. Britton													G					

TABLE 4A. Continued

Species / Association / Plot	F			S			Pa			Ps			D			G		
	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S	N	C	S
Orthotrichum consimile Mitt.														B				
Rhytidiopsis robusta Broth.														G				
Mnium orthorhynchium Brid.														W				
M. spinulosum Br. & Sch.														W				
Brachythecium collinum Schp.														G				
Bryum sandbergii Holz.														G				
Pseudoisothecium stoloniferum (Hook.) Grout														G				
Camptothecium pinnatifidum (Sull. & Lesq.) Jaeg. & Sauerb.															GR			
C. aeneum (Mitt.) Jaeg. & Sauerb.															R			
Antitrichia curtipendula (Hedw.) Brid.															R			
Anacolia menziesii f. *grandifolia* Grout															R			
Eurhynchium stokesii (Smith) Schp.															G			
Neckera menziesii Hook.															R			
Orthotrichum sp.															R			
Rhacomitrium heterostichum v. *sudeticum* (Funck.) Jones															R			
Hedwigia ciliata (Hedw.) Pal. Beauv.															R			
Lophozia sp.															R			
Porella cordeana (Hueben.) Evans.															R			
Mnium venustum Mitt.													G		GR			
Brachythecium velutinum (L.) Br. & Schp.														BWG			G	
Camptothecium lutescens v. *occidentale* Ren. & Card.															X			W
Mnium insigne Mitt.																G		
Brachythecium erythrorhizon Schp.																G		
Drepanocladus uncinatus v. *symmetricus* (R. & C.) Grout.																B		
Calliergoniella schreberi (Willd., Br. & Sch.) Grout																G	G	
Eurhynchium substrigosum v. *barnesii* (R. & C.) Grout																	G	
Dicranum scoparium Hedw.																	G	
Dicranoweisia cirrhata (Hedw.) Lindb.																		W
Ptilidium pulcherrimum (Weber) Hampe																		W
Scapania umbrosa (Schrader) Dumortier																		W

TABLE 4B. Distribution and Habitats of Fungi found in Study Plots

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest	Volume of Fruit Bodies Least-Average-Largest	Distribution: Association, Plot
Myxomycetes							
Exosporeae							
Ceratiomyxales							
Ceratiomyxaceae							
Ceratiomyxa fruticulosa (Müll.) Macbr.	Prev.	W	SM	B–E–g			PaN, PsC, DS, GS.
C. fruticulosa v. *porioides* Lister	Prep.	W	SM	B–A–a			PsC.
Myxogasteres							
Liceales							
Liceaceae							
Tubifera ferruginosa (Batsch.) J. F. Gmel.	Prep.	W	SM	C–C–a			DN.
Reticulariaceae							
Lycogala epidendrum (L.) Fr.	App.	W	SM	H–E–g			PsC, DS.
Reticularia lycoperdon Bull.	App.	W	SM	B–A–a			DS, GS.
Trichiales							
Trichiaceae							
Arcyria incarnata (Pers.) Pers.	Prep.	W	SM	B–C–a			PaN.
A. nutans (Bull.) Grev.	Prep.	W	SM	C–C–a			DN.
A. pomiformis (Leers) Rost.	Prep.	W	SM	B–C–a			PaN.
Trichia favoginea (Batsch.) Pers.	Prep.	W	SM	A–C–a			PsC.
Trichia sp.	Prep.	W	SM	B–C–a			PsC.
Stemonitales							
Stemonitaceae							
Enerthenema melanospermum Macbr. & Mart.	Prep.	W	SM	B–C–a			PaN.
Stemonitis flavogenita Jahn	Prep.	W	SM	H–C–a			PaS, GN.
Physarales							
Physaraceae							
Fuligo septica (L.) Macbr.	Prep.	L	SM	D–A–a			GS.
Physarum cinereum (Batsch.) Pers.	Prep.	L	SM	A–C–c			DS.
P. ?rubiginosum Fr.	Prep.	W	SM	C–C–a			GN.
P. bivalve Pers.	Prep.	L	SM	C–C–c			SS.
Leocarpus fragilis (Dicks.) Rostk.	Prev.	L	SM	B–C–d			DN, DC, GC.
Didymiaceae							
Diderma sp.	Prep.	L	SM	B–C–c			PsN.
Mucilago spongiosa (Leyss.) Morg.	Prep.	L	SM	C–C–c			SC.
Didymium minus (Lister) Morg.	Prep.	L, C	SM	B–C–a			DC.
Phycomycetes							
Oomycetes							
Peronosporales							
Peronosporaceae							
Peronospora claytoniae Farl.	Prep.	P	L	C–A–c			DS.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest	Volume of Fruit Bodies Least-Average-Largest	Distribution: Association, Plot
Albuginaceae							
Albugo tragopogonis (Pers.) ex S. F. Gray	Prep.	P	L	C–C–a			PaC.
Pythiaceae							
Pythium debaryanum Hesse	App.	S	M	C–A–b			SC, PaN.
P. rostratum Butler	Prep.	S	M	C–A–b			PsS.
P. vexans de Bary	Prep.	S	M	C–A–b			PsN, PsC, DN.
Zygomycetes							
Mucorales							
Mucoraceae							
Absidia glauca Hagen	Prep.	S	M	C–A–b			PsS.
Mucor geophilus Oud.	Prep.	S	M	C–A–b			DS.
Mucor janseni Lendner	Prep.	S	M	C–A–b			PsN.
Choanephoraceae							
Cunninghamella echinulata Thaxter	Prep.	S	M	C–A–b			PsS.
Mortierellaceae							
Mortierella pusilla Oud.	Prep.	S	M	C–A–b			PsS.
Mortierella sp.	Prep.	S	M	C–A–b			PaN.
Ascomycetes							
Hemiascomycetes							
Exoascales							
Taphrinaceae							
Taphrina populi-salicis Mix.	Prep.	P	L	B–C–a			PsN.
T. confusa (Atk.) Gies.	Prep.	P	L	C–A–a			SC.
T. potentillae (Farl.) Johans.	Prep.	P	L	C–A–a			SC.
Euascomycetes							
Plectomycetes							
Eurotiales							
Eurotiaceae							
Thielavia sepedonium Emmons	Prep.	SC	M	C–A–b			SC.
Onygenaceae							
Onygena corvina Alb. & Schw.	Prep.	D	P	B–C–c			GC.
Erysiphales							
Erysiphaceae							
Microsphaera penicillata (Wallr. ex Fr.) Lév.	Prep.	P	L	J–F–a			PsN.
M. diffusa Cke. & Pk.	Prep.	P	L	J–F–a			PsN.
Sphaerotheca pannosa (Wallr. ex Fr.) Lév.	Prep.	P	L	C–C–a			DC.
Sphaeriales							
Claviceptaceae							
Claviceps purpurea (Fr.) Tul.	Prep.	P	T–5	J–F–a			FN, SN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest	Volume of Fruit Bodies Least-Average-Largest	Distribution: Association, Plot
Xylariaceae							
Rosellinia medularis (Wallr.) Ces. & deNot.	Prep.	W	T–5	D–C–a			SS.
Xylaria hypoxylon (L. ex Fr.) Grev.	Prev.	W	T–5	B–C–f	4 36 125		DC, DS.
Hypocreales							
Hypocreaceae							
Hypomyces chrysospermus Tul.	App.	F	T–5	B–C–d			PaN.
H. lactifluorum (Schw.) Tul.	App.	F	T–5	H–C–e			GS.
Nectriaceae							
Nectria cinnabarina (Tode) Fr.	Prep.	P?	T–5	A–C–a			DC.
Pseudosphaeriales							
Pseudosphaeriaceae							
Dibotryon morbosum (Schw.) Thiess. & Syd.	App.	P	T–5	F–E–d			PsC, DS.
Didymellina iridis (Desm.) v. Hoehn.	Prep.	P	L	D–A–b			SS.
Sordaria bombardioides Auersw.	Prep.	D	T–5	A–C–b			GS.
Hysteriales							
Hysteriaceae							
Hysterographium fraxini (Pers. ex Fr.) deNot.	Prep.	W	T–5	B–C–c			DC.
Propolis faginea (Schw.) Karst.	Prep.	P?	T–5	K–E–c			SN, DS.
P. leonis (Tul.) Rehm.	Prev.	T	T–5	I–G–d			PaN, PaC, PaS, DC, GN.
Rhytisma salicinum Pers. ex Fr.	Prep.	P	L	B–C–b			GN.
Hypodermataceae							
Lophodermium tumidum (Fr.) Rehm	Prev.	P?	L	M–A–g			SC, PsS, GS.
L. pinastri (Schrad. ex Fr.) Chev.	Prev.	P?	L	M–E–g			PaC, PsN, PsC, DS, GN.
Discomycetes							
Helotiales							
Helotiaceae							
Chlorociboria aeruginosa (Fr.) Seaver	Prep.	W	T–5	C–A–c			GS.
Dasyscypha calycina Fckl.	Prep.	P?	T–5	B–A–b			GC.
D. ciliata Hahn	App.	W, L	T–5	K–E–g			DN, DC, GC.
D. patula (Pers. ex Fr.) Sacc.	Prep.	L	T–5	D–A–b			DS.
D. subtilissima Cke.	Prep.	L	T–5	A–C–b			PaN.
Helotium sp.	Prep.	L	T–5	B–C–a			GS.
H. caudatum (Karst.) Velen.	Prep.	L	T–5	E–C–f			DS.
H. citrinum Fr.	Prev.	W	T–5	K–C–g			DN, DC, GN, GS.
H. cyathoideum (Bull. ex Fr.) Karst.	Prep.	W	T–5	I–C–a			PsN, SS.
H. herbarum (Pers. ex Fr.) Fr.	Prev.	L	T–5	E–C–f			SS.
H. lutescens Fr.	Prep.	L	T–5	A–C–b			PsN.
H. virgultorum (Vahl. ex Fr.) Karst.	Prev.	L	T–5	K–C–g			SN, SC, SS, PsN, PsC, DN, DC, GN, GC.
Mollisia carduorum (Rehm) A. L. Smith	App.	L	T–5	E–C–g			SS, GN.
M. ?stictella Sacc. & Speg.	Prep.	L	T–5	A–C–b			SS.
Rutstroemia sp.	Prep.	L	T–5	A–C–a			PsC.
Trichoscyphella tenuipilosa Cash	Prep.	P?	T–5	N–C–g			PsN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Hyaloscyphaceae											
Lachnum sp.	Prep.	L	T–5	D–A–b							DS.
L. leucophaeum (Pers. ex Fr.) Karst.	Prep.	L	T–5	I–A–f							SN, GC.
L. virginellum (Cke.) Rehm	Prep.	L	T–5	B–A–c							PsN.
L. virgineum (Batsch. ex Fr.) Karst.	Prep.	W	T–5	B–A–b							DC.
Geoglossaceae											
Microglossum fumosum Durand	Prep.	L	T–4	B–C–a							GC.
Mitrula abietis Fr.	Prev.	L	T–4	L–C–g	6	312	620	0.07	0.30	0.63	DN, DC, DS, GC, GS.
Spathularia flavida Fr.	Prev.	L	T–4	O–C–g	6	105	330	0.39	1.72	3.93	DC, GN, GC, GS.
Pezizales											
Pezizaceae											
Discina ancilis (Pers.) Sacc.	Prev.	L	T–4	C–A–b	1			50.3			DN.
Humarina semiimmersa (Karst.) Seaver	Prev.	G	T–4	B–A–c							GN.
Otidea alutacea (Fr.) Bres. v. *alutacea*	Prep.	G	T–4	B–C–b	109			58.9			DN.
O. alutacea var. *microspora* Kanouse	App.	G	T–4	H–C–f	23	32	40	21.2	93.4	235.6	DN.
O. leporina (Fr.) Fckl. v. *leporina*	Prev.	G	T–4	H–C–g	18	24	30	4.71	12.96	29.45	DN, DC, DS, GN, GC.
O. leporina v. *minor* (Rehm) Sacc.	Prep.	G	T–4	B–C–a	65			3.53			DC.
O. onotica (Fr.) Fckl.	Prev.	G	T–4	B–C–d	5	100	291	4.71	12.4	21.2	PsN, DS, GN.
Patella theleboloides (Alb. & Schw.) Seaver	App.	D	T–4	H–A–g							PaS, PsC.
Peziza vesiculosa Bull. ex Fr.	App.	D	T–4	H–E–d							PaS, PsC.
Pseudoplectania nigrella (Fr.) Fckl.	App.	G	T–4	N–A–g	1	16	48	3.14	4.96	7.07	DN, GN, GC, GS.
Ascobolaceae											
Ascobolus stercorarius (Fr.) Schroet.	App.	D	T–4	H–A–g							PaS, PsC.
Saccobolus violaceus Boud.	Prep.	D	T–4	B–A–a							PaS.
Helvellaceae											
Morchella angusticeps Pk.	Prep.	G	T–4	B–C–b	2			18.85			DN.
M. esculenta Pers. ex Fr.	Prep.	G	T–4	C–A–b	1			18.85			DN.
Helvella esculenta Fr.	Prep.	G	T–4	H–A–c	1			60.4			PsN, DS.
H. infula Fr.	App.	G	T–4	H–E–g	1	1	2	25.1	146.1	384.8	PsC, DC.
H. lacunosa Fr.	Prev.	G	T–4	O–C–g	4	19	60	12.57	253.37	461.8	PsN, DS, GN, GS.
Basidiomycetes											
Heterobasidiomycetes											
Uredinales											
Melampsoraceae											
Coleosporium solidaginis (Schw.) Thuem.	App.	P	L	C–C–a							SC, GN.
Cronartium coleosporoides (Diet. & Holw.) Arth.	Prep.	P	L	I–D–e							PsN, GC.
C. ribicola Fisch.	Prep.	P	L	C–C–a							DC.
Pucciniastrum goeppertianum (Kuehn.) Kleb.	Prep.	P	L	D–A–b							FS.
P. myrtilis (Schum.) Arth.	Prep.	P	L	D–B–a							GC.
Uredinopsis macrosperma (Cke.) Magn.	Prep.	P	L	D–B–a							GS.
Hyalopsora polypodii (Pers.) Magn.	Prep.	P	L	N–A–f							DS.
Melampsora arctica Rostr.	Prep.	P	L	B–C–b							GN.
M. occidentalis Jackson	Prep.	P	L	B–C–a							PsN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least Average-Largest	Volume of Fruit Bodies Least-Average-Largest	Distribution: Association, Plot
Pucciniaceae							
Cumminsiella mirabilissima (Pk.) Nannf.	Prev.	P	L	K–E–g			PaC, PsN, PsC, DS, GN, GC.
Phragmidium ivesiae Syd.	Prev.	P	L	N–G–g			FN, FC, SC, PaC, PsN.
P. montivagum Arth.	Prev.	P	L	N–D–g			FC, FS, SN, SC, SS, PsN, PsS, DS, GN, GC.
P. rosae-acicularis Liro	Prev.	P	L	O–G–g			SC, SS, PsN, PsS, DC.
P. speciosum (Fr.) Cooke	App.	P	L	J–E–b			SN, SS, PsN.
Gymnosporangium bethelii Kern	Prep.	P	L	J–D–e			PaS.
Uromyces heterodermus Syd.	Prep.	P	L	B–A–c			GC.
U. probus Arth.	Prep.	P	L	C–A–b			FC.
Puccinia atrofusca (Dudl. & Thomps.) Holw.	Prep.	P	L	B–A–b			PaN.
P. balsamorhizae Pk.	Prev.	P	L	N–D–e			SS, PaS, DS.
P. cirsii Lasch.	Prev.	P	L	N–F–a			SC, SS, PaC, PsN, DC.
P. coronata Corda	App.	P	L	J–F–a			FC, PaC, DS, GC.
P. crandallii Pam. & Hume	Prev.	P	L	N–G–g			FN, FC, FS, SC, PaN, PsN, DN, DC, GC.
P. grindeliae Pk.	Prev.	P	L	N–A–f			FC, SC.
P. heucherae (Schw.) Diet.	Prep.	P	L	N–D–g			SC, DS.
P. hieracii (Schum.) Mart.	Prep.	P	L	B–A–c			FN.
P. iridis (DC.) Wallr.	Prev.	P	L	C–C–a			FN, FC, PaC.
P. jonesii Pk. v. *jonesii*	App.	P	I	N–A–f			FC, SC, PaC, PsS, DS.
P. levellei Mont.	Prep.	P	L	H–A–c			SC, SS.
P. pimpinellae (Str.) Mart.	App.	P	L	D–D–d			DC.
P. rubefaciens Johans.	Prev.	P	L	I–D–g			SN, SS, PsN, DS.
P. rubigo-vera (DC.) Wint.	Prep.	P	L	C–C–a			PsN.
P. rubigo-vera v. *apocrypta* (Ell. & Tr.) Arth.	App.	P	L	I–A–f			PaN, PaS, PsN, DN.
P. vagans (DC.) Arth. v. *vagans*	Prep.	P	L	D–C–a			FC.
P. vagans v. *gayophytii* Arth.	Prev.	P	L	D–D–a			FC.
Ustilaginales							
Ustilaginaceae							
Ustilago bullata Berk.	App.	P	L	J–F–a			FN, PaN, PaS.
Tilletiaceae							
Entyloma compositarum Farl.	Prep.	P	L	C–A–b			FC.
Tremellales							
Tulasnellaceae							
Tulasnella violea (Fr.) Bourd. & Galz.	Prep.	W	T–3	D–C–b			PsN.
Tremellaceae							
Exidia recisa (S. F. Gray) Fr.	Prep.	W	T–3	D–A–c			GS.
E. saccharina Fr.	App.	W	T–3	H–E–f			PsC, GN.
E. spiculosa (S. F. Gray) Somm.	App.	W	T–3	C–E–b			DS, GN.
Phlogiotis helvelloides (Pers.) Martin	Prev.	G	T–3	K–C–f	1 4 10	9.42 13.2 28.3	DS, GC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Pseudohydnum gelatinosum (Fr.) Karst.	Prev.	W	T–3	E–C–g	4	34	47	9.42	9.81	14.1	DC, DS, GC, GS.
Tremella mesenterica (S. F. Gray) Pers.	Prep.	W	T–3	E–C–b							DS, GS.
Tremella sp.	Prep.	W	T–3	C–A–b							PsN.
Sebacina sp.	Prep.	W	T–3	B–A–b							GC.
Dacrymycetaceae											
Calocera cornea (Fr.) Lk.	App.	W	T–3	K–E–f							PaS, DS, GN.
C. viscosa (Fr.) Fr.	App.	G	T–3	B–C–f	1	1	2	0.35			GC.
Guepiniopsis merulinus (Pers.) Pat.	Prev.	W	T–3	O–E–g							PsC, DC, DS, GN, GS.
Dacrymyces abietinus (Pers.) Schroet.	Prev.	W	T–3	L–E–g							PsN, PsC, DS, GN.
D. deliquescens Duby	Prev.	W	T–3	K–E–g							PaS, PsC, DN, DC, DS, GC.
D. ellisii Coker	Prep.	W	T–3	C–C–a							DC.
D. palmatus (Schw.) Bres. *apud* Hoehn.	Prev.	W	T–3	K–E–g							PaC, PaS, DN, DS, GN, GC, GS.
D. punctiformis Neub.	App.	W	T–3	N–E–g							PaN, PaS, DS, GN, GC.
Homobasidiomycetes											
Aphyllophorales											
Cyphellaceae											
Cyphella alboviolascens (A. & S. ex Fr.) Karst.	App.	L	T–5	A–C–c							GN, GC.
C. capula (Holmsk. ex Fr.) Fckl.	Prep.	L	T–5	E–C–b							SN, SS.
Cyphella sp.	Prep.	L	T–4	D–C–b							SS.
Leptotus retirugis (Bull. ex Fr.) Karst.	Prev.	M	T–5	E–C–g							PsC, DS.
Solenia ochracea Pers. ex Fr.	Prep.	L	T–5	D–A–b							PsN.
Corticiaceae											
Aleurodiscus sp.	Prep.	W	T–5	B–A–c							DS.
A. amorphus (Pers.) Rab. ex Cke.	App.	W	T–5	E–C–f							GN.
Corticium sp.	Prep.	W	T–5	A–C–c							PsN.
Corticium sp.	Prep.	W	T–5	B–A–b							GN.
C. bicolor (Fr.) Bres.	Prep.	W	T–5	B–C–a							GC.
C. furfuraceum Bres.	Prep.	W	T–5	B–A–b							GN.
C. livido-caeruleum Karst.	Prep.	W	T–5	B–A–b							GS.
C. polygonium Pers. ex Fr.	Prep.	W	T–5	D–A–a							DC.
C. subseriale Bourd. & Galz.	Prep.	W	T–5	B–A–b							PaS.
C. udicola Bourd.	Prev.	W	T–5	O–C–g							SN, SC, SS, PsN.
Pellicularia sp.	App.	W	T–5	E–E–f							DS, GN.
P. subcoronata (Hoehn. & Litsch.) Rogers	Prev.	W	T–5	E–E–g							PaN, PsN, DN, DC.
P. vaga (Berk. & Curt.) Rogers	Prep.	W	T–5	E–E–f							PsN, DN.
Peniophora sp.	Prep.	W	T–5	A–C–b							PsC, DC.
Peniophora sp.	Prep.	W	T–5	B–A–b							PsC.
P. affinis Burt	Prep.	W	T–5	B–A–b							DS.
P. amoena Burt	Prep.	W	T–5	C–C–b							GS.
P. carnosa Burt	Prep.	W	T–5	B–C–a							PaS.
P. cinerea (complex)	Prep.	W	T–5	B–A–b							PaN, PaS, PsN.
P. cremea Bres.	Prep.	W	T–5	O–E–f							PaN, PaS, DS, GN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
P. gracillima Ell. & Ev.	Prep.	W	T–5	E–E–d							DN.
P. greschikii (Bres.) Bourd. & Galz.	Prep.	W	T–5	A–C–c							GN.
P. ?hastata Litsch.	Prep.	W	T–5	B–A–b							DN, GC.
P. luna Rom.!!	App.	W	T–5	A–C–f							PsC.
P. mollis (Fr. *sensu* Bres.) Bourd. & Galz.	Prep.	W	T–5	B–A–b							DN, DC, GC.
P. sanguinea (Fr.) Hoehn. & Litsch.	App.	W	T–5	E–E–g							GN, GC.
P. tenuis (Pat.) Massee	App.	W	T–5	B–A–b							GN.
Vararia granulosa (Pers. ex Fr.) Laurila	Prep.	W	T–5	D–A–b							GN.
Thelephoraceae											
Thelephora caryophyllea Schaeff. ex Fr.	Prep.	G	T–5	H–E–g	2	5	10	1.57	13.2	21.2	PaN, PsN, DC, GN, GC.
T. intybacea Fr.	App.	W	T–5	B–C–a							PsN, GC.
T. terrestris Ehr. ex Fr.	Prev.	W	T–5	C–A–d							PsN. DN, GC.
Tomentella echinospora (Ellis) Bourd. & Galz.	App.	W	T–5	I–A–b							GN, GC.
T. fusca (Pers.) Schroet.	Prep.	W	T–5	B–C–b							DS.
Stereaceae											
Hymenochaete cinnamomea (Pers.) Bres.	Prep.	W	T–5	B–A–a							DN.
H. tabacina (Sow. ex Fr.) Lév.	Prev.	W	T–5	O–E–g							PsN, DN, DC, DS, GN, GC, GS.
Stereum hirsutum Willd. ex Fr.	Prep.	W	T–5	O–C–c							SN, GS.
S. lobatum (Kunze) Fr.	Prep.	W	T–5	A–C–b							PsC.
S. patelliforme Burt.	App.	W	T–5	E–C–f							SN, PsN, PsC.
S. sanguinolentum (Alb. & Schw.) Fr.	Prev.	W	T–5	N–E–g							PaS, PsN, PsS, DN, DC, DS, GN, GC.
Meruliaceae											
Merulius testator Fr.	Prep.	W	T–5	B–C–a							PaN.
M. tremellosus Schrad. ex Fr.	App.	W	T–5	B–C–d							GS.
Phlebia albida Fr.	Prep.	W	T–5	I–A–b							PsC, DC.
Coniophoraceae											
Coniophora arida Fr.	Prep.	W	T–5	B–C–a							PsC.
Coniophorella olivacea (Fr.) Karst.	Prep.	W	T–5	B–C–b							PsC.
Serpula americana (Burt) W. B. Cke.	Prep.	W	T–5	B–A–b							PsC.
Clavariaceae											
Cladaria amythestina (Fr.) Ritgen	Prep.	G	T–2	B–A–c	2			35.3			FS.
Clavaria fusiformis (Fr.) Corner	Prep.	G	T–2	B–C–b	16			0.49			GN.
C. pulchra Pk.	Prep.	G	T–2	C–C–b							PsN.
C. (nr.) *cystidiophora* Kauffman	Prep.	G	T–2	A–C–b							GN.
Clavariadelphus ligulus (Fr.) Donk	Prev.	G	T–2	O–C–g	14	185	581	0.59	6.35	31.42	PsN, DN, GN, GS.
C. maricola (Kauff.) Doty n.c.	Prep.	G	T–2	B–C–b	5			0.49			DC.
C. truncatus (Quel.) Donk	Prev.	G	T–2	H–E–g	1	22	55	3.14	140.1	395.8	PsN, GN.
C. unicolor (Rav. ex Berk.) Doty n.c.	Prep.	G	T–2	B–C–c	56			14.14			DC.
Clavariella abietina (Fr.) Karst.	Prev.	G	T–2	I–C–g	7	28	58	7.07	45.9	137.4	PaC, PsN, PsC, DC, GN, GC.
C. acris (Pk.) Doty n.c.	Prev.	G	T–2	B–C–g	21	25	29	2.36	9.16	15.7	DC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
C. apiculata (Fr.) Karst.	Prep.	G	T–2	C–C–b							DN.
C. botrytis (Fr.) Singer	Prep.	G	T–2	A–C–b							GS,
C. pinicola (Burt) Doty n.c.	Prep.	G	T–2	B–C–b	18			37.7			PsN.
C. subdecurrens (Coker ss. Doty) Doty n.c.	Prev.	G	T–2	N–C–g	1	187	1057	1.57	8.72	21.2	PsN, PsS, DN, DC, GN, GC.
C. suecica (Fr.) Karst.	Prep.	G	T–2	C–C–b							PaS.
Clavaria spp.	Prep.	G	T–2	E–C–d	2	44	192	0.39	1.1	2.36	DC, GN, GC, GS.
Donkella corniculata (Fr.) Doty n.c.	Prep.	G	T–2	B–C–b	1			2.36			GN.
Cantharellaceae											
Cantharellus cibarius Fr.	Prep.	G	T–2	B–C–b	9			100.5			GC.
Hydnaceae (ss. lat.)											
Auriscalpium vulgare (Fr.) S. F. Gray	Prev.	C	T–5	O–E–g	3	29	204	22.0			PaC, PaS, PsN, PsC, PsS, DC, DS, GN, GS.
Dentinum repandum (Fr.) S. F. Gray	App.	G	T–2	H–C–d	1	15	17	75.4	180.1	307.9	GN.
Grandinia farinacea (Fr.) Bourd. & Galz.	Prep.	W	T–5	B–A–b							GN.
Mucronella aggregata Fr.	Prep.	W	T–4	D–C–b							PsN.
Odontia arguta (Fr.) Quél.	Prep.	W	T–5	B–C–b							GS.
O. bicolor (Alb. & Schw.) Bres.	Prep.	W	T–5	B–A–b							GS.
O. crustosa (Fr.) Quél.	Prev.	W	T–5	B–E–d							PaS, DC, DS.
O. fimbriata Fr.	Prep.	W	T–5	B–C–b							GN.
Polyporaceae (ss. lat.)											
Coltricia perennis (L. ex Fr.) S. F. Gray	Prev.	G	T–5	K–E–g	2	4	8	1.57	3.85	12.57	PaN, PaS, GN, GC, GS.
Coriolus hirsutus (Wulf. ex Fr.) Quél.	Prep.	W	T–5	B–C–a							DS.
C. versicolor (L. ex Fr.) Quél.	Prep.	W	T–5	E–E–b							DS.
Cryptoporus volvatus (Pk.) Hubbard	App.	W	T–5	N–A–g							PaC, PsS, DC.
Daedaleopsis confragosa (Pers. ex Fr.) Schroet.	Prep.	W	T–5	F–C–d							GS.
Fomes annosus (Fr.) Cke.	App.	W	T–6	C–A–a							PsN, DS.
F. officinalis (Fr.) Lloyd	Prep.	W	T–6	A–C–b							PaS.
F. pinicola (Sw. ex Fr.) Cke.	Prev.	W	T–6	O–E–g							DC, DS, GN, GC, GS.
F. subroseus (Weir) Overh.	Prev.	W	T–6	O–E–g							DN, DC, DS.
Gloeophyllum americanum (Overh.) W. B. Cke.	Prep.	W	T–5	J–C–f							GC.
G. sepiarium (Wulf. ex Fr.) Karst.	App.	W	T–5	N–E–d							PsN, DS, GC,
Gloeoporus dichrous (Fr.) Bres.	App.	W	T–5	F–C–f							PsN, DC, DS.
Hapalopilus rutilans (Fr.) Karst.	App.	W	T–5	B–C–a							SN, SC.
Hirschioporus abietinus (Dicks. ex Fr.) Donk	Prev.	W	T–5	O–E–g							PsN, PsC, PsS, DN, DC, DS, GN, GC, GS.
Onnia tomentosa (Fr.) Karst.	App.	W	T–5	B–E–e	1		2				PsN, GS.
Phaeolus schweinitzii (Fr.) Pat.	App.	W	T–5	E–C–g	1	3	6	7068.8	618321	1413780	PsS, DC, GC.
Phlebiella candidissima (Schw.) W. B. Cke.	Prep.	W	T–5	B–A–b							GC.
Polyporus elegans (Bull.) Fr.	Prev.	W	T–5	K–E–g	3	5	10	5.03	21.4	37.7	DC, GN, GC, GS.
P. picipes Fr.	App.	W	T–5	C–C–d	1		2	28.3	51.14	115.5	DC, GN.
Polyporus spp.	Prep.	W	T–5	B–E–d							PaS, PsS, GC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Poria bombycina (Fr.) Cke.	App.	W	T–5	B–E–b							GS.
P. carbonica Overh.	Prep.	W	T–5	F–C–f							DC, GN.
P. ferrea (Pers.) Bourd. & Galz.	Prep.	W	T–6	A–C–a							GS.
P. lenis (Karst.) Sacc.	App.	W	T–5	B–A–b							DS, GN.
P. subacida (Fr.) Cke.	Prep.	W	T–6	B–A–b							GC.
P. versipora (Pers.) Baxter	Prep.	W	T–5	C–C–b							DS.
Poria spp.	Prep.	W	T–5	A–C–b							GS.
Poria sp.	Prep.	W	T–5	D–A–a							GN.
Porodaedalea pini (Thore ex Fr.) Murr.	Prep.	W	T–6	N–C–d							DN, GC.
Trametes carbonaria (Berk. & Curt.) Overh.	Prev.	W	T–5	B–E–d							PsS, GN, GS.
Tyromyces anceps (Pk.) Murr.	Prep.	W	T–5	C–A–c							PsS.
T. caesius (Schrad. ex Fr.) Murr.	Prev.	W	T–5	K–C–g							PaN, DN, DC, DS, GN.
T. fragilis (Fr.) Donk	Prev	W	T–5	K–E–g							PsC, DC, DS, GN.
T. undosus (Pk.)Murr.	Prep.	W	T–5	B–C–e							GC.
Agaricales											
Hygrophoraceae											
Hygrophorus agathosmus Fr.	Prep.	G	T–2	A–C–b	10			2.01			DN.
H. albidus Karst.	Prep.	G	T–2	A–C–b	12			88.0			PaS.
H. chrysodon Fr.	Prev.	G	T–2	O–E–g	3	31	151	3.14	70.3	226.2	PaN, PaC, PaS, PsN, PsC, PsS, DC, DS, GN, GC, GS.
H. conicus Fr.	Prev.	G	T–2	H–E–g	1	12	39	3.9	84.35	196.4	FC, FS, SC, PaN, PaC, PaS, DS, GN.
H. eburneus Fr.	Prev.	G	T–2	N–C–g	6	30	112	75.4	772.14	4712.4	PaN, PaC, PsN, PsC, PsS, DN, GN, GC.
H. gliocyclus Fr.	Prep.	G	T–2	A–C–b							PsS.
H. inocybeformis A. H. Smith f.	App.	G	T–2	A–C–d							DN, GS.
H. miniatus Fr.	App.	G	T–2	B–E–e	1	2	3	4.71	9.4	14.1	FS, GS.
H. paludosus Pk.	Prev.	G	T–2	H–C–g	3	145	578	18.81	360.65	1539.4	PsC, DN, DC, DS, GN, GC, GS.
H. parvulus Pk.	Prep.	G	T–2	A–C–b	3	109	312	25.1	291.8	815.3	GS.
H. pratensis Fr.	Prev.	G	T–2	B–C–g							PaN, PaC, PsN, PsC, PsS, GC.
H. pusillus Pk.	Prep.	G	T–2	A–C–b							PaS.
H. speciosus Fr.	Prev.	G	T–2	H–C–g	15	63	84	38.5	320.4	890.6	GN, GC.
H. virgineus Fr.	Prep.	G	T–2	A–C–b	1			62.8			GS.
Hygrophorus 22615	Prep.	G	T–2	B–C–b	6			196.4			PsN.
Hygrophorus 22647	Prep.	G	T–2	B–C–b	3			137.4			GN.
Hygrophorus 21447	Prev.	G	T–2	B–C–d	4	7	9	15.7	31.39	42.4	FS, PsN, GN.
Hygrophorus 21630	Prev.	G	T–2	B–C–d	1	3	4	63.6	146.1	251.3	PaN, PaS, PsN.
Hygrophorus 24714	Prep.	G	T–2	C–C–b							PsN.
Tricholomataceae											
Armillaria mellea Vahl. ex Fr.	Prev.	P?	T–2	N–C–g	1	29	77	50.3	529.8	1767.2	PaC, DC, GN, GC, GS.
Armillaria 19856	Prep.	G	T–2	B–A–e	2			76.96			GN.
Clitocybe candicans (Fr.) Lange	Prep.	G	T–2	A–C–b	5			14.7			GS.
C. clavipes (Fr.) Quél.	Prep.	G	T–2	A–C–a	2			62.8			GS
C. cyathiformis (Fr.) Quél.	Prep.	G	T–2	A–C–e	3			117.8			DS.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
C. dilapoda (Fr.) Gill.	App.	G	T–2	A–C–d	5			14.7	15.9	17.2	PsC, DS.
C. peltigerina Pk.	Prev.	G	T–2	H–C–d	1	981	7002	0.25	8.41	78.5	PaN, PaS, PsN, DN, GN, GC.
C. concava (Fr.) Gill.	Prev.	G	T–2	A–C–d	2	9	13	14.1	48.2	117.8	SN, GS.
C. ?rivulosa (Pers.) Quel.	Prep.	G	T–2	A–C–c	34			62.8			DS.
C. serrulata v. *pithyophila* ss. Lange	Prep.	G	T–2	A–C–b	5			14.7			PsN.
Clitocybe spp. (indet.)	?	G	T–2	A–C–b	1	16	59	1.57	34.27	117.8	FN, PaS, PsC, DC, GC, GS.
Clitocybe 19853	Prep.	G	T–2	B–A–c	2			12.57			GN.
Clitocybe 19528	Prep.	G	T–2	B–A–b	2			21.2			PaS.
Clitocybe 20672	Prep.	G	T–2	B–C–a	1			6.28			PsS.
Clitocybe 21098	Prep.	G	T–2	B–C–a	5			15.7			DC.
Clitocybe 22826	Prep.	G	T–2	B–C–c	1			21.2			PaC.
Clitocybe 20806	Prep.	G	T–2	B–C–a	1			5.3			GN.
Clitocybe 21941	Prep.	G	T–2	B–C–b	4			87.96			DC.
Clitocybe 22730	Prep.	G	T–2	B–C–b	1			14.7			SC.
Clitocybe 22151	App.	G	T–2	B–C–b	1	3	5	3.53	22.9	42.4	PsS, GS.
Clitocybe 22478	App.	G	T–2	B–C–b	1	4	6	21.2	25.1	28.9	SC, GN.
Clitocybe 22004	Prep.	G	T–2	B–C–b	1			9.42			PaC.
Clitocybe 22607	Prep.	G	T–2	B–C–b	2			18.85			PsN.
Clitocybe 21185	App.	G	T–2	B–C–a	2	2	3	5.3	9.7	14.1	SS, PaC.
Clitocybe 22441	App.	G	T–2	B–C–b	20	30	39	117.8			PsN, DN.
Clitocybe 22441B	App.	G	T–2	B–C–b	2	2	2	24.1	51.3	78.5	DN, GN.
Clitocybe 22661	Prev.	G	T–2	H–C–f	8	27	46	12.57	44.76	75.4	PsN, PsC.
Clitocybe 22288	Prev.	G	T–2	B–C–b	2	12	22	21.2	60.5	117.8	DN, DS, GN.
Clitocybe 21203	Prev.	G	T–2	B–C–d	1	4	10	21.2	70.1	117.8	FS, SC, PaC, PaS,
Clitocybe 20975	Prev.	G	T–2	B–C–e	1	4	8	5.3	28.0	58.9	PaC, PsC, GC.
Clitocybe 22525	App.	G	T–2	B–C–c	4	16	28	9.42	21.9	35.3	SN, GN.
Clitocybe 21065	Prev.	G	T–2	B–C–d	2	4	7	28.3	47.5	98.2	PsC, PsS, DS, GC.
Clitocybe 21079	Prev.	G	T–2	B–C–d	2	14	39	9.42	61.56	117.8	PaN, GC.
Clitocybe 20912	Prev.	G	T–2	H–C–g	3	25	80	18.8	68.0	157.1	PsN, PsC, PsS, DN, DC, DS, GN.
Clitocybe 20905	Prev.	G	T–2	B–C–g	1	5	10	3.53	50.5	117.8	SC, PaS, PsN, PsC, PsS, DN, DC, GC.
Clitocybe 20786	Prev.	G	T–2	B–C–g	7	46	119	12.57	40.8	98.2	PsN, PsC, DC, GN.
Clitocybe 21112	Prev.	G	T–2	B–C–g	1	23	77	28.3	186.3	603.2	FN, PaC, PsN, PsC, D3, GN, GC.
Clitocybe 21109	Prev.	G	T–2	H–C–g	1	18	58	9.4	121.4	471.2	SN, SS, PaN, PaC, PsN, PsC, PsS, DN, DC, GN, GC.
Clitocybe 24390	Prep.	G	T–2	C–C–a	2			3.14			PsN.
Clitocybe 24584	Prep.	G	T–2	C–C–b	1			18.85			GN.
Clitocybe 24442	App.	G	T–2	C–C–d	5	6	8	28.3	35.4	42.4	DC, GS.
Clitocybe 24585	Prev.	G	T–2	C–C–b	1	2	4	9.42	18.6	37.7	PaS, DS, GN.
Clitocybe 24547	App.	G	T–2	C–C–b	4	7	10	8.84	28.47	48.1	PsN, GN.
Clitocybe 23557	App.	G	T–2	C–E–e	1	1	1	9.4	12.56	15.71	DS, GC.
Clitocybe 23424	Prep.	G	T–2	C–A–b	100			50.3			PaC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Clitocybe 21908	Prep.	G	T–2	B–C–b	5			2.36			DC.
Clitocybe 20992	Prep.	G	T–2	B–C–a	1			42.4			PsC.
Clitocybe 22356	App.	G	T–2	B–C–b	1	2	4	28.26	45.5	62.8	DN, GS.
Clitocybe 19861	Prev.	G	T–2	B–E–g	2	4	6	2.36	26.6	58.9	PsC, DN, DC.
Clitocybe 25168	Prep.	G	T–2	D–A–b							FS.
Clitocybe 18737	Prep.	G	T–2	A–C–b							PaS.
Clitocybe 26028	Prep.	G	T–2	D–A–a							DS.
Collybia albipilata Pk.	Prev.	C	T–2	O–C–g	1	241	1417	0.59	10.21	117.8	PaC, PsN, PsC, PsS, DN, DC, DS, GN, GC, GS.
C. cirrhata (Fr.) Quél.	Prep.	G	T–2	A–C–c	28			3.14			PsN.
C. conigena (Fr.) Quél.	Prev.	C	T–2	F–C–d	2	22	58	0.66	3.62	8.84	PsC, DN, GC.
C. cookii (Bres.) Arnold	App.	C	T–2	A–C–b	2	94	185	0.29	1.72	3.14	PsN, DS.
C. cylindrospora Kauffm.	Prep.	G	T–2	C–C–b							PsN.
C. fulvipes Murrill	Prev.	G	T–2	O–E–g	1	98	320	0.39	11.1	100.5	PaS, PsC, PsS, DN, DC, DS, GN, GC, GS.
C. ?oyes (Fr.) Fr.	Prep.	G	T–2	A–C–c	1			6.28			SC.
C. plexipes (Fr.) ss. Kauffman	Prep.	G	T–2	E–C–e	16			15.7	39.3	62.8	PaN, PaC.
C. racemosa (Pers. ex Fr.) Berk.	Prev.	G	T–2	B–C–d	2	12	21	0.79	8.7	28.3	PaS, PsN, DN, GN.
C. tuberosa (Fr.) Quél.	Prep.	G	T–2	C–C–b	6			10.6			PsN.
C. dryophila (Fr.) Quél.	Prev.	G	T–2	H–E–g	1	33	125	1.18	52.4	98.2	FN, FS, SC, PsN, DC, GN, GS.
Collybia 19576	Prev.	G	T–2	B–E–g	1	2	5	0.98	5.63	18.85	FN, SC, PaN, PsN, PsC, DS, GN.
Collybia 22755	Prep.	G	T–2	B–C–e	1			62.8			DC.
Collybia 21494	Prep.	G	T–2	B–C–b	1			18.85			GN.
Collybia 21466	Prep.	G	T–2	B–C–b	3			15.7			GN.
Collybia 20991	Prev.	G	T–2	B–C–d	1	2	3	3.14	5.76	8.84	PaS, PsN, DS.
Collybia 22579	Prep.	G	T–2	B–C–b	1			62.8			PsN.
Collybia 21451	Prep.	G	T–2	B–C–b	2			35.3			GN.
Collybia 21331	Prep.	G	T–2	B–C–b	5			12.57			DS.
Collybia 22217	Prep.	G	T–2	B–C–b	3			8.84			SS.
Collybia 22150	App.	G	T–2	B–C–b	5			8.84	22.1	35.3	PsC, PsS.
Collybia 20884	Prep.	G	T–2	B–C–a	3			4.71			PsN.
Collybia 21835	Prep.	G	T–2	H–C–b	2	3	4	19.6	47.5	75.4	SC, PaN.
Collybia 19822	Prep.	G	T–2	B–A–c	8			28.3			SN.
Collybia spp. (indet.)	?	G	T–2	H–C–d	2	12	47	7.07	26.1	62.8	FN, PaN, PaS, PsN, DN, DS, GN, GC, GS.
Collybia 22314	Prep.	G	T–2	B–C–b	2			8.84			DS.
Collybia 18618	Prev.	G	T–2	A–C–f				351.9			FN, GC, GS.
Laccaria laccata (Fr.) Berk. & Br.	Prev.	G	T–2	O–C–g	2	129	309	18.85	113.5	282.7	DN, GN, GC, GS.
Lentinus omphalodes Fr.	Prep.	G	T–2	A–C–c	19			0.59			SN.
Leucopaxillus amarus f. *bicolor* (Murr.) Singer & Smith	Prev.	G	T–2	K–C–g	4	37	195	12.57	550.71	4071.5	PaS, PsN, PsC, DN, DC, GN, GC.
L. giganteus (Fr.) Singer	Prep.	G	T–2	B–C–b	3			1077.5			PsC.
Lyophyllum 21495	Prep.	G	T–2	B–C–b	1			49.5			GN.
Lyophyllum 21696	Prev.	G	T–2	B–C–d	1	5	14	4.71	26.1	42.4	FN, SN, SC, PsC, DN.
Lyophyllum 21487	Prev.	G	T–2	B–C–d	1	3	6	24.5	38.2	75.4	PaC, DC, GN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Lyophyllum 22786	Prep.	G	T–2	B–C–c	1			7.07			DC.
Lyophyllum 20779	Prep.	G	T–2	B–C–a	3			21.2			GN.
Lyophyllum 22278	Prep.	G	T–2	B–C–b	3			48.1			PaS.
Lyophyllum 21778	App.	G	T–2	B–C–b	3	12	20	35.3	55.4	75.4	SN, PsC.
Lyophyllum 21892	Prep.	G	T–2	B–C–b	3			42.4			DC.
Lyophyllum 20788	App.	G	T–2	B–C–a	17	28	38	12.57	14.14	15.7	DC, GN.
Lyophyllum 18823	App.	G	T–2	A–C–b	6			2.65	3.98	5.3	SS. GS,
Marasmius androsaceus Fr.	Prev.	L	T–4	O–E–g	8	138	598	0.59	2.95	10.6	PaN, PsN, PsC, PsS, DN, DC, DS, GN, GC, GS.
M. chordalis Fr.	App.	G	T–2	M–C–b	1			7.07			DS, GS.
M. epiphyllus Fr.	Prev.	L	T–4	E–C–d	24	130	261	0.047	0.596	0.942	FS, SC.
M. fuscopurpureus Fr.	Prev.	G	T–2	O–E–g	3	162	1244	8.84	57.46	235.6	PaN, PaC, PsN, PsC, DN, DC, DS, GC, GS.
M. perforans Fr.	Prev.	L	T–4	K–E–g	9	215	714	0.21	2.26	5.3	DS, GN, GS.
M. piceinus Kauffman	Prev.	L	T–4	O–C–g	621	40256	118128	0.11	0.44	0.94	DN, DC, GN, GC.
M. rotula Fr.	Prep.	L	T–4	B–C–a	6			0.29			PsN.
Marasmius 19744	Prep.	G	T–2	B–A–c	5			0.37			GS.
Marasmius 20875	Prep.	G	T–2	B–C–a	3			2.36			PsN.
Marasmius 21340	Prep.	G	T ?	B–C–b	2			1.57			DS.
Marasmius 21698	Prep.	G	T–2	B–C–b	2			9.42			FN.
Marasmius 22411	Prep.	G	T–2	B–C–b	24			12.57			DN.
Marasmius 22672	Prep.	G	T–2	B–C–b				28.3			PsC.
Mycena abramsii Murr.	Prep.	G	T–2	A–C–c	14			2.36			PaS.
Mycena adonis (Fr.) Quél.	App.	G	T–2	F–C–g	3	16	37	0.79	1.6	2.51	DC, DS, GS.
M. albidula (Pk.) Smith	App.	G	T–2	E–E–c	1	10	16	0.29	4.99	14.1	SC, DN.
M. alcalina (Fr.) Quél.	Prep.	G	T–2	C–C–c							DS.
M. amabilissima (Pk.) Sacc.	Prev.	G	T–2	K–C–g	10	170	742	0.14	4.75	24.5	PaS, PsN, PsC, DN, DC, DS, GC, GS.
M. atralboides (Pk.) Sacc.	Prev.	G	T–2	O–C–g	8	291	1005	0.59	12.07	18.85	PsC, DN, DC, DS, GN, GC, GS.
M. atrocyanea (Fr.) Gill.	App.	G	T–2	E–C–f	2		3	1.54	2.6	3.14	FN, FS, PaC, DN.
M. aurantiidisca Murr.	Prep.	G	T–2	B–C–a	76			6.28	7.56	8.84	GS.
M. blumanea (Fr.) Quél.	Prep.	G	T–2	B–C–b							PsC.
M. capillaripes Pk.	App.	G	T–2	E–C–g	14	24	34	1.51	18.04	62.8	PsC, DS, GS.
M. capillaris (Fr.) Quél.	App.	G	T–2	A–C–b	6	15	31	0.59	1.26	2.51	SN, SS.
M. cinerella Karst.	App.	G	T–2	E–C–g	61	145	229	1.57	13.55	42.4	SC, DN.
M. citrinomarginata Gill.	Prev.	G	T–2	O–E–g	2	27	134	0.59	5.86	18.85	PaS, PsN, PsC, DN, DC, DS, GS.
M. clavicularis (Fr.) Gill.	App.	G	T–2	C–C–g							PaS, DS.
M. concolor (Lange) Kühner	Prep.	G	T–2	D–C–a							SC.
M. constans Pk.	App.	G	T–2	K–C–g	2	32	88	0.59	21.2	78.54	PaS, DS, GN, GS.
M. ?debilis (Fr.) Gill.	Prep.	G	T–2	D–C–a							PsN.
M. delicatella (Pk.) Smith	Prev.	G	T–2	O–C–g	15	69	140	0.59	3.56	23.6	FN, SC, DN, DC, DS, GN, GC, GS.
M. elegantula Pk.	Prev.	W	T–2	O–E–g	7	63	316	2.35	25.07	100.5	PaN, PsN, PsS, DN, DC, DS, GN, GC, GS.
M. epipterygioides Pearson	Prev.	G	T–2	O–C–g	11	192	646	3.93	18.5	49.5	SC, PaS, PsN, PsC, PsS, DN, DC, DS, GN, GC, GS.
M. filopes (Fr.) Quél.	App.	G	T–2	E–C–f	2	5	8	0.49	4.24	8.84	SN, SC, PsC, DS, GS.
M. flavoalba (Fr.) Quél. v. *flavoalba*	Prep.	G	T–2	E–E–c	1		2	1.57			PsS, GC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
M. flavoalba v. *microspora* Smith	Prep.	G	T–2	A–C–b	9			3.14			GS.
M. fragillima Smith	App.	G	T–2	L–C–g	1	5	14	7.07	26.49	56.5	PaS, PsN, PsC, DN, DS.
M. fragillissima Smith	Prep.	G	T–2	C–C–a							DC.
M. fusipes Murr.	Prev.	G	T–2	A–C–f	4	17	41	0.79	26.23	35.3	DS, GC, GS.
M. gracilis (Fr.) Kuhner	Prep.	G	T–2	A–C–c	7			0.59			DN.
M. iodiolens Lundell	Prep.	G	T–2	D–C–a							SC.
M. leptocephala (Fr.) Quél. v. *leptocephala*	Prev.	G	T–2	O–C–g	1	29	81	0.98	14.16	70.7	PaC, PaS, PsN, PsC, DN, DC, DS, GN, GC, GS.
M. leptocephala v. *ammoniaca* Smith	Prep.	G	T–2	B–C–a	10			8.84			DC.
M. lilacifolia (Pk.) Smith	Prep.	W	R–2	B–A–b	3			2.36			PsC.
M. maculata Karst.	Prep.	G	T–2	B–C–a	22			62.8			GS.
M. mauritanica (Maire) Kühner	Prep.	G	T–2	B–A–c	8			2.34			FS.
M. metata (Fr.) Quél.	Prev.	G	T–2	O–C–g	5	121	486	1.26	14.17	150.8	PaN, PaC, PaS, PsN, PsC, PsS, DN, DC, DS, GN, GC, GS.
M. ?olivaceo-brunnea A. H. Smith	Prep.	G	T–2	B–C–a	6			0.39			SC.
M. oregonensis Smith	Prep.	G	T–2	A–C–b	?			2.36			GS.
M. parabolica (Fr.) Quél. ss. Kauffman	App.	G	T–2	E–C–f	5	4	5	44.2	50.1	56.6	SC, SS, DN.
M. pectinata Murr.	App.	G	T–2	A–C–f	3	13	24	18.8			SS, DN.
M. piceicola Smith	Prep.	G	T–2	O–C–g	6	8	10	18.8	56.1	86.6	PsN, DS, GN.
M. plicosa (Fr.) Gill.	Prev.	G	T–2	B–C–f	2	16	57	7.07	18.7	35.3	PaS, DN, DC, DS, GN.
M. plumbea (Fr.) Sacc. v. *plumbea*	Prev.	G	T–2	K–C–g	1	32	130	1.5	17.69	57.7	FN, FS, SN, SC, SS, PaC, PaS, PsC, DN, DC, GC.
M. plumbea v. *robusta* Smith	Prev.	G	T–2	E–C–f	2	66	167	9.82	39.59	70.7	FN, FC, FS, SN, SC, SS, PaN, PaC, PsN, GC, GN.
M. pseudoclavicularis Smith	Prev.	G	T–2	O–C–f	7	307	698	2.36	9.76	25.1	PaN, PaS, DS.
M. pseudotenax Smith	Prev.	G	T–2	B–C–g	10	12	15	10.6	21.9	39.3	PaN, PsN, PsC.
M. purpureofusca Pk.	Prev.	W	T–2	O–E–g	12	56	134	0.79	13.57	70.7	PaN, PaC, PaS, PsN, PsC, DN, DC, DS, GN, GC, GS.
M. pusilla Smith	Prep.	G	T–2	B–C–a	4			3.14			DS.
M. pura (Fr.) Quél.	Prev.	G	T–2	O–E–g	1	57	159	1.57	33.72	196.4	FS, PaN, PaC, PaS, PsN, PsC, PsS, DN, DC, DS, GN, GC, GS.
M. rosella (Fr.) Quél.	Prev.	G	T–2	O–C–g	99	671	2808	1.13	8.08	49.5	PaN, PaS, DN, DC, DS, GN, GC.
M. stannea (Fr.) Quél.	Prev.	G	T–2	O–E–g	1	13	48	2.36	26.93	75.4	FN, SN, SC, PaN, PaC, PaS, PsC, PsS, DS, GN, GS.
M. subaquosa Smith	Prep.	G	T–2	B–C–a	11			70.7			GS.
M. subcana Smith	Prep.	G	T–2	B–C–e	3			12.57			DN.
M. subplicosa Karst.	Prev.	G	T–2	E–C–g	12	104	320	0.37	13.26	34.4	PaC, PaS, PsN, PsC, DN, DC, DS, GN, GC, GS.
M. subvitrea Smith	Prep.	G	T–2	E–C–b	4	6	9	8.83	9.7	10.6	FN, PsC.
M. tenella (Fr.) Quél.	Prep.	G	T–2	A–C–b	28			78.5			SS.
M. vulgaris (Fr.) Sacc.	Prev.	G	T–2	K–C–g	14	34	74	2.36	18.91	153.9	DC, GN, GC.
Mycena spp. (unidentifiable)	?	G	T–2	O–E–g	2	258	451	0.21	4.97	12.37	SC, PaN, PaC, PsN, DN, DC, DS, GN, GC, GS.
Mycena spp. (Identifications incomplete)	?	G	T–2	K–E–g	1	76	354	0.08	11.39	28.3	SC, PaN, PaC, PsC, DN, DS, GN, GS.
Omphalina 20787	Prep.	G	T–2	B–C–a	4			7.07			GN.
Omphalina 21721	App.	G	T–2	B–C–b	1	11	21	28.3	31.8	35.3	FN, SC.
Omphalina 21642	Prep.	G	T–2	B–C–b	14			2.36			PaN.
Omphalina 19578	Prev.	G	T–2	H–E–g	1	14	38	0.25	1.35	3.53	FN, FS, SN, PaN, PaC, PaS, PsN.
Omphalina 22562	Prep.	G	T–2	B–C–b	4			4.71			GN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Omphalina 19787	Prep.	G	T–2	B–A–c	8			39.3			FS.
Omphalina 19753	App.	G	T–2	B–A–c	4	9	14	1.57	5.24	12.57	PsN, GS.
Omphalina 24810	Prep.	G	T–2	J–C–c							SC, DN.
Panellus mitis (Pers. ex Fr.) Singer	App.	G	T–2	O–C–g							DN, DC, GN.
Pleurotus candidissimus Berk. & Curt.	Prev.	G	T–2	K–E–g							DC, GN, GC.
Pleurotus 19791	Prev.	G	T–2	H–F–f	12	23	42	0.16	11.41	62.8	FC, FS, SC, DC.
Pleurotus 21610	Prep.	G	T–2	B–C–b							PsN.
Pleurotus 22160	Prep.	G	T–2	B–C–b	8			3.03			PsS.
Pleurotus 18891	Prep.	G	T–2	A–C–c							PsC.
Tricholoma imbricatum (Fr.) Quél.	Prev.	G	T–2	E–C–b	14	49	103	78.5	631.4	1393.6	PsS, DN.
T. personatum (Fr.) Berk.	Prev.	G	T–2	B–E–b	2	3	3	137.4	299.3	452.4	SC, SS, PsN.
T. terreum (Schaeff. ex Fr.) Kickx	Prev.	G	T–2	O–E–g	7	143	814	1.57	72.31	157.1	SN, PaN, PaC, PaS, PsN, PsC, DN, DC, DS, GN, GC, GS.
T. chrysites (Jungh.) Gill.	Prep.	G	T–2	A–C–b	11			21.2			GS.
T. myomyces sensu Lange	Prep.	G	T–2	A–C–c				12.57			DS.
Tricholoma 22798	Prep.	G	T–2	B–C–c	10			62.8			DC.
Tricholoma 21165	Prev.	G	T–2	B–C–g	1	2	4	1.5	9.81	12.57	SS, PaS, DC, GC.
Tricholoma 20760	Prev.	G	T–2	B–C–g	2	3	4	2.36	48.72	150.8	SN, SC, PsN, DC, DS, GN.
Tricholoma 20751	Prev.	G	T–2	B–C–g	1	6	15	15.7	92.8	169.6	DC, GN, GC.
Tricholoma 19648	Prev.	G	T–2	B–E–d	1	13	30	2.36	24.25	75.4	PaN, DS, GN, GC.
Tricholoma 21129	Prev.	G	T–2	B–E–g	2	2	3	15.7	78.8	169.6	DC, GC.
Tricholoma 20759	App.	G	T–2	B–C–d	1			14.1	46.3	78.5	GN.
Tricholoma 21853	App.	G	T–2	B–C–f	4			87.96	94.23	100.5	DC.
Tricholoma 22774	Prep.	G	T–2	B–C–c	2	5	8	6.28	28.29	50.3	DC, GC.
Tricholoma 21381	Prep.	G	T–2	B–C–a	18			301.6			FS.
Tricholoma 21844	Prep.	G	T–2	B–C–b	4			2.36			DC.
Tricholoma 21382	Prep.	G	T–2	B–C–a	1			9.4			FS.
Tricholoma 21496	Prep.	G	T–2	B–C–b	2			62.8			GN.
Tricholoma 22821	Prep.	G	T–2	B–C–c	3			42.4			DC.
Tricholoma 19601	Prep.	G	T–2	B–A–b	5			35.3			PaC.
Tricholoma 22216	Prep.	G	T–2	B–C–b	1			230.9			SS.
Tricholoma 22429	Prep.	G	T–2	B–C–b	20			21.2			DN.
Tricholoma 21977	Prep.	G	T–2	B–C–b	45			117.8			PaC.
Tricholoma 21512	App.	G	T–2	B–C–b	3	10	17	54.98	186.55	502.7	PsN, GN.
Tricholoma 22848	Prep.	G	T–2	B–C–c	10			706.9			PaC.
Tricholoma 22536	Prep.	G	T–2	B–C–b	15			565.5			PaN.
Tricholoma 23432	App.	G	T–2	C–E–d	10			14.1	32.2	50.3	DN, DC.
Tricholoma 24371	Prep.	G	T–2	C–C–d	1	3	8	6.28	13.61	18.85	PaN, GN, GS.
Tricholoma 24352	App.	G	T–2	C–C–d	1	2	4	7.07	11.39	15.7	DN, GN.
Tricholoma 24869	Prep.	G	T–2	C–C–a	1			15.7			GN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Xeromphalina campanella (Fr.) Kühner & Maire	Prep.	G	T–2	E–C–a	350						GS.
X. pubescentipes (Pk.) Kuehn. & Maire	Prev.	G	T–2	O–E–g	2	249	1108	2.36	15.23	157.1	FN, SC, PsN, PsS, DN, DC, DS, GN, GC.
Leucosporeae spp. (undetermined)	?	G	T–2	H–E–g	2	52	332	0.02	31.52	346.4	FN, FC, FS, SN, SC, SS, PaN, PaC, PaS, PsN, PsC, DN, DC, DS, GN, GC, GS.
Amanitaceae											
Pluteus cervinus (Fr.) Quél.	App.	G	T–2	K–E–d	1	2	3	4.71	119.1	226.2	PsN, DC, GC.
Agaricaceae											
Agaricus campestris Fr.	Prep.	G	T–2	B–C–a	1			21.2			FC.
A. diminutivus Pk.	Prev.	G	T–2	B–C–d	1	4	6	12.57	49.28	117.8	PaS, DC, GC.
A. hondensis Murr.	Prep.	G	T–2	B–C–b	1			62.8			DS.
A. silvicola (Vitt.) Fr.	App.	G	T–2	B–C–d	5	6	7	15.7	334.6	950.3	DC.
Cystoderma cinnabarina (Alb. & Schw. ex Secr.) Fayod.	App.	G	T–2	E–C–d	1	10	20	9.42	47.64	98.2	PaS, DS, GN.
C. fallax Singer & Smith	Prev.	G	T–2	O–C–g	9	69	296	5.3	73.6	230.9	PaN, PaC, PsN, PsC, PsS, DN, DC, GN, GC.
C. granulosa (Batsch. ex Fr.) Fayod	Prev.	G	T–2	O–E–g	1	28	50	1.57	33.12	117.8	PaN, PaC, PaS, PsN, PsC, PsS, DN, DC, DS, GN, GC.
L. clypeolaria (Fr.) Quél.	Prev.	G	T–2	L–C–d	1	24	138	42.4	162.1	577.3	PsS, DC, GN, GC, GS.
Lepiota 21952	App.	G	T–2	B–C–b	2		3	28.3	109.2	190.1	PsN, DC.
Lepiota 21099	Prep.	G	T–2	B–C–a	4			63.6			DC.
Lepiota 21364	App.	G	T–2	B–C–d				9.4	21.4	35.3	PaS.
Lepiota 21319	App.	G	T–2	H–C–b	1	5	9	12.56	25.93	39.3	DS.
Lepiota 21318	Prep.	G	T–2	B–C–b	10			125.7			DS.
Lepiota 21315	Prep.	G	T–2	B–C–b	4			12.57			DS.
Lepiota 21219	Prep.	G	T–2	B–C–a	3			2.36			SC.
Lepiota 21125	Prep.	G	T–2	B–C–a	9			35.3			DC.
Lepiota 21767	Prep.	G	T–2	B–C–b				169.6	183.0	196.4	PsC.
Lepiota 21869	Prev.	G	T–2	B–C–f	2	4	6	12.57	22.88	35.3	DC, DS.
Lepiota 21863	Prep.	G	T–2	B–C–b	8			125.7			DC.
Lepiota 21695	App.	G	T–2	B–C–b	1			28.3	73.1	117.8	FN, PsC.
Lepiota 21356A	App.	G	T–2	B–C–b	1			35.3	42.8	50.3	PaS.
Lepiota 21730	Prev.	G	T–2	B–C–b	2	12	19	24.5	29.7	35.3	FC, SN, SS, DC.
Lepiota 20713	Prev.	G	T–2	H–C–g	1	44	44	2.36	33.92	137.5	SN, SC, SS, PaS, DC, DS, GN.
Coprinaceae											
Coprinus cordisporus Gibbs	Prep.	G	T–2	B–A–c	1			0.39			PaS.
C. ephemereus Fr.	Prev.	G	T–2	B–E–g	1	4	12	2.36	10.2	18.8	SN, SS, PaS.
C. narcoticus Fr.	Prep.	G	T–2	A–C–a	15			0.39			PsC.
C. niveus Fr.	Prep.	G	T–2	B–A–c	3			12.57			PsC.
C. plicatilis Fr.	Prep.	G	T–2	B–A–b	1			3.93			PaC.
C. radians	Prep.	G	T–2	B–A–b	3			15.7			DC.
Coprinus 20823	Prep.	L	T–2	B–C–a	10			2.36			FN.
Coprinus 21324	App.	G	T–2	B–C–a	2			78.7			DC, DS.
Coprinus AHS 22387	Prep.	D	T–2	B–C–a							FC.
Coprinus spp.	?	GD	T–2	B–C–g				9.42	107.15	274.9	SS, PsC, DC, DS.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Panaeolus acuminatus Schaeff. ex Fr.	App.	G	T–2	B–C–d	1	2	4	1.5	4.28	7.07	FS, PaS.
P. campanulatus (Fr.) Quél.	Prev.	D	T–2	B–E–g	1	11	45	39.3	110.1	255.3	FN, SS, PaS, PsC.
P. coprophilus Smith	Prep.	D	T–2	B–C–b	2			2.36			FS.
P. foensicii (Fr.) S. F. Gray	Prep.	D	T–2	B–A–c	6			56.5			PsC.
P. atrifolia (Pk.) Smith	Prev.	G	T–2	B–E–g	1	17	66	24.5	94.3	197.6	FN, SN, DC, DS.
P. agrariella Atk.	Prev.	G	T–2	B–C–a	2		3	24.5	26.4	28.3	SC, SS, PaC.
P. candolleana (Fr.) Smith	App.	G	T–2	B–C–a	1	20	36	424.1	486.9	549.8	PaS, DC.
Panaeolus sp. 1	Prep.	G	T–2	B–C–c	1			8.84			PaC.
P. limicola (Pk.) Smith	App.	G	T–2	B–C–c	3			8.84	13.77	18.7	SS.
P. obtusata (Fr.) Smith	Prep.	G	T–2	B–C–a	2			18.85			PsC.
Panaeolus sp. 2	Prep.	D	T–2	B–C–a	10			0.14			PaC.
Panaeolus sp. 3	Prev.	G	T–2	B–E–g	3			56.55			SN, DS.
Psathyrella nr. AHS 14037	Prep.	G	T–2	B–C–b							FN.
Psathyrella AHS 4990	Prep.	G	T–2	B–C–b							SC.
Psathyrella AHS 25644	Prep.	G	T–2	B–C–a							SS.
Psathyrella nr. No. 5	Prep.	G	T–2	B–C–a							DC.
Bolbitiaceae											
Conocybe siliginea Smith	Prep.	G	T–2	B–A–c	9			2.36			FS.
C. spicula f. *spicula*	Prep.	G	T–2	A–C–a	4			1.01			PsC.
C. tenera (Fr.) Quél.	Prep.	G	T–2	A–C–c	1			15.7			PaC.
Conocybe 21745	App.	G	T–2	B–C–b	8			2.65	4.47	6.28	SN, SC.
Strophariaceae											
Flammula nr. *spumosa* Fr.	Prep.	G	T–2	B–C–b	3			50.3			PsC.
Flammula 22059	Prev.	G	T–2	B–C–b	7	24	49	42.4	55.4	78.5	PsS, DS, GC, GS.
Flammula 22069	App.	G	T–2	B–C–b	2	6	10	50.3	84.1	117.8	PsS, GC.
Flammula 22025	Prep.	G	T–2	B–C–b	6			98.2			GC.
Flammula 22471	Prep.	G	T–2	B–C–b	1			48.1			GN.
Flammula 21932	Prep.	G	T–2	B–C–b	7			35.3			DC.
Flammula 24873	Prep.	G	T–2	C–C–c	11			28.3			PsC.
Flammula 24745	Prep.	G	T–2	C–C–b	63			12.57			GN.
Kuehneromyces cookii Smith ined.	Prep.	L	T–2	A–C–b	12			9.42			GS.
Kuehneromyces 24734	App.	L	T–2	C–C–c	2		3	42.4	120.0	197.6	PsN, DN.
Naematoloma capnoides (Fr.) Karst.	App.	W	T–2	B–C–f	5	48	92	196.4	416.3	636.1	PsS, GC.
Pholiota adiposa Fr.	Prep.	W	T–2	B–C–b	13			117.8			GC.
Pholiota erinacea (Fr.) Karst.	Prep.	L	T–2	E–C–f	8	13	17	0.039	0.804	1.57	DC, GN.
Pholiota 22240	Prep.	G	T–2	B–C–b	7			117.8			PaS.
Pholiota 22186	Prev.	G	T–2	B–C–d	1	3	5	50.3	61.1	82.8	PaN, GN, GC.
Pholiota 21076	App.	G	T–2	B–C–e	3	5	7	62.8	69.1	75.4	DC, GC.
Pholiota 21037	Prev.	G	T–2	B–C–g	1	22	78	62.8	93.7	117.8	PsC, GC.
Pholiota 21061	Prep.	G	T–2	B–C–a	6			56.5			GC.
Psilocybe coprophila (Fr.) Quél.	Prep.	D	T–2	B–C–a	12			14.1			FS.
P. subviscida (Pk.) Kauffman	Prep.	D	T–2	B–A–b	8			3.93			PsC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Psilocybe sp.	Prep.	D	T–2	B–C–c							PsC.
Stropharia aeruginosa (Fr.) Quél.	Prev.	G	T–2	B–C–g	1	5	20	24.1	67.1	117.8	FN, FC, SN, SS, DS.
S. semiglobata Fr. v. *semiglobata*	Prep.	D	T–2	B–C–e	7			49.5			PaS.
S. semiglobata v. *stercoraria* (Fr.) Smith	App.	D	T–2	B–E–f	13			42.4	53.0	63.6	PsC.
Cortinariaceae											
Cortinarius 22682	Prep.	G	T–2	B–C–b	10			75.4			PsC.
Cortinarius 22485	Prep.	G	T–2	B–C–b	2			75.4			GN.
Cortinarius 21742	Prep.	G	T–2	B–C–b	6			42.4			SN.
Cortinarius 21091	Prep.	G	T–2	B–C–a	3			12.57			DC.
Cortinarius 20761	Prep.	G	T–2	B–C–a	2			49.5			GN.
Cortinarius 19662	Prep.	G	T–2	B–A–b	5			75.4			GS.
Cortinarius 21605	Prep.	G	T–2	B–C–b	2			100.5			PsN.
Cortinarius 21459	Prep.	G	T–2	B–C–b	1			125.7			GN.
Cortinarius 22825	Prep.	G	T–2	B–C–c	2			282.7			PaC.
Cortinarius 22075	Prep.	G	T–2	B–C–b	2			402.1			GC.
Cortinarius 21549	Prep.	G	T–2	B–C–b	3			230.9			GN.
Cortinarius 21768	Prep.	G	T–2	B–C–b	1			699.8			PsC.
Cortinarius 20814	Prep.	G	T–2	B–C–a	2			1130.97			GN.
Cortinarius 22125	Prep.	G	T–2	B–C–b	6			384.8			PsS.
Cortinarius 21036	Prep.	G	T–2	B–C–a	12			117.8			GC.
Cortinarius 20810	Prep.	G	T–2	B–C–a	4			502.7			GN.
Cortinarius 21516	Prep.	G	T–2	B–C–b	6			665.2			GN.
Cortinarius 21547	Prep.	G	T–2	B–C–b	2			75.4			GN.
Cortinarius 20955	Prep.	G	T–2	B–C–a	3			75.4			DN.
Cortinarius 22779	Prep.	G	T–2	B–C–c	1			169.65			DC.
Cortinarius 21473	Prep.	G	T–2	B–C–b	5			50.3			GN.
Cortinarius 22645	Prep.	G	T–2	B–C–b	29			75.4			PaN.
Cortinarius 22504	Prep.	G	T–2	B–C–b	1			950.3			GN.
Cortinarius 20811	App.	G	T–2	B–C–d	2	3	4	28.3			GN, GS.
Cortinarius 21551	App.	G	T–2	B–C–b	1			62.8	69.1	75.4	GN, GS.
Cortinarius 19855	Prep.	G	T–2	B–A–c	1			269.4			GN.
Cortinarius 21762	App.	G	T–2	B–C–b	25			381.7	756.4	1131.0	PaC, PsC.
Cortinarius 22505	App.	G	T–2	B–C–f	1			94.2	117.8	141.4	PaC, GN.
Cortinarius 21572	App.	G	T–2	B–C–f	2	3	5	56.5	72.3	88.0	PsN, GC.
Cortinarius 21470	App.	G	T–2	B–C–f	3		4	42.4	58.9	75.4	DC, GN.
Cortinarius 22067	App.	G	T–2	B–C–f	1			176.7	187.2	197.6	GN, GC.
Cortinarius 21756	App.	G	T–2	B–C–b	13	46	79	381.7	1327.2	2429.1	PsN, GN.
Cortinarius 21543	App.	G	T–2	B–C–b	4	19	33	226.2	699.8	1017.9	PaC, PsC.
Cortinarius 19621	Prev.	G	T–2	B–E–g	2	5	8	0.59	4.03	7.07	DC, GN, GS.
Cortinarius 22003	Prev.	G	T–2	B–C–f	1	4	7	35.3	45.3	50.3	PaN, PaC, DC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Cortinarius 20780	Prev.	G	T–2	B–C–g	2	3	5	42.4	71.5	117.8	PsS, GN, GS.
Cortinarius 21810	App.	G	T–2	B–C–b	6	29	52	230.9	248.2	265.5	PsC, DN.
Cortinarius 19598	Prep.	G	T–2	B–C–b	5			137.4			PsC.
Cortinarius 20765	Prev.	G	T–2	B–C–g	1	3	5	5.3	19.9	75.4	SS, PaN, PsC, PsN, DS, GN.
Cortinarius 20752	Prev.	G	T–2	B–C–g	1	3	6	19.2	157.2	282.7	PsN, PsS, GN, GC.
Cortinarius 21445	Prev.	G	T–2	B–C–g	1	4	11	62.8	95.8	157.1	PsN, DC, GN, GS.
Cortinarius 20722	App.	G	T–2	B–C–a	1			35.3	78.3	157.1	PsN, GN.
Cortinarius 22174	Prep.	G	T–2	B–C–b	36			1017.9			PsS.
Cortinarius 21800	Prev.	G	T–2	B–C–b	1	3	4	25.1	69.8	197.6	PsC, DS, GC, GS.
Cortinarius 19810B	Prev.	G	T–2	B–E–g	3	9	14	12.57	40.08	98.2	PsN, DC, GN, GS.
Cortinarius 20818	Prev.	G	T–2	B–C–a	3	29	88	9.42	40.88	75.4	PsN, DC, GN, GC.
Cortinarius 20712	Prev.	G	T–2	B–C–g	2	5	11	28.3	104.9	294.5	DS, GN.
Cortinarius 19569	Prep.	G	T–2	B–E–d	8	22	48	35.3	74.1	137.4	DN, GN, GC.
Cortinarius 20725	App.	G	T–2	B–C–d	2	17	31	141.4	579.7	1017.9	GN.
Cortinarius 22173	Prep.	G	T–2	B–C–b	60			62.8			PsS.
Cortinarius 21593	Prev.	G	T–2	B–C–f	5	33	79	28.3	85.6	145.2	PsN, PsC, PsS, DC, GN, GC.
Cortinarius 20718	Prev.	G	T–2	B–C–g	1	4	10	28.3	84.5	226.2	PsN, PsS, DC, GN, GC, GS.
Cortinarius 21348	Prev.	G	T–2	B–C–g	6	19	29	50.3	54.1	75.4	PaN, PsS, DN, DC, GC.
Cortinarius 19810A	Prev.	G	T–2	B–E–g	1	6	21	35.3	82.9	169.6	SN, PaC, PsN, PsS, DC, GC, GS.
Cortinarius 20757	App.	G	T–2	B–C–d	4	41	101	87.92	416.46	1017.9	PsS, GN.
Cortinarius 20729	Prev.	G	T–2	B–C–d	5	29	76	98.2	554.1	2474.0	PsS, GN, GC.
Cortinarius 21561	Prep.	G	T–2	B–C–b	33			269.4			PsN.
Cortinarius 20816	Prev.	G	T–2	B–C–g	4	13	25	35.3	83.1	157.1	PaN, PaC, PsN, DN, GN, GC.
Cortinarius 20716	Prev.	G	T–2	B–C–d	3	20	62	49.5	235.53	636.5	PsN, PsS, GN.
Cortinarius 20838	Prev.	G	T–2	B–C–g	1	40	194	35.3	77.4	137.4	PaN, PsN, PsS, DN, DC, DS, GN, GC, GS.
Cortinarius 19572	Prev.	G	T–2	B–C–g	1	104	238	2.36	42.47	197.6	PaN, PsN, DN, DC, DS, GN, GC, GS.
Cortinarius 19599	Prev.	G	T–2	B–E–g	11	128	636	2.34	99.93	351.9	PaC, PsN, DN, DC, GN, GC, GS.
Cortinarius 25251	Prep.	G	T–2	D–A–b	4	149	545	11.0	23.2	35.4	PaC.
Cortinorius 18609	Prep.	G	T–2	A–C–b	79	223	621				GS.
Cortinarius sp.	Prep.	G	T–2	D–C–a							DC.
Galerina badipes sensu Kuehner	App.	G	T–2	A–C–f	4	30	55	12.57	14.66	15.7	DS, GS.
G. camerina sensu Kuehner	Prep.	G	T–2	A–C–c	5			56.5			SC.
G. hypnorum sensu Atkinson	Prep.	G	T–2	A–C–b	2			5.65			DS.
G. hypnorum sensu Kuehner	Prep.	G	T–2	A–C–c	7			1.41			PsC.
G. hypnorum sensu Lange	Prep.	G	T–2	A–C–c	2			0.38			FS.
G. rubiginosa sensu Kuehner	Prep.	G	T–2	A–C–b	3			3.13			PaS.
G. semilanceata (Pk.) A. H. Smith	Prep.	G	T–2	A–C–c	33			18.85			DS.
G. vittaeformis sensu Lange	Prev.	G	T–2	A–C–f	6	14	18	3.14			SC, PaS, DS.
Galerina 19543	Prev.	G	T–2	A–E–g	31	47	75	1.18	15.7	50.3	SN, SS, PsC.
Galerina 19674	Prev.	G	T–2	A–E–f	2	6	13	9.42	24.1	50.3	SN, PsC, DC.
Galerina 19806	Prev.	G	T–2	A–E–g	1	15	58	0.58	13.47	62.8	PaC, PsC, PaS, DC, DS, GN, GC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest	Volume of Fruit Bodies Least-Average-Largest	Distribution: Association, Plot
Galerina 19577	Prev.	G	T–2	A–E–g	7 25 56	2.36 14.1 49.5	SN, PaN, PsN, PsC, DN, DC, DS, GN, GC, GS.
Galerina 20789	Prev.	G	T–2	A–C–g	3 48 186	0.59 4.25 15.7	FN, FC, FS, SN, SC, PaS, PaN, PsS, DN, DS, GN, GC.
Galerina 19673	Prep.	G	T–2	B–A–b	2	0.59	SN.
Galerina 21993	Prep.	G	T–2	B–C–b	10	7.07	PaC.
Galerina 23329	?	G	T–2	C–E–g	2 55 259	0.39 7.1 35.3	SN, SC, PaN, PaC, PsN, PsC, DN, DC, GN.
Hebeloma crustuliniforme sensu lato	Prev.	G	T–2	K–C–g	2 102 360	1.57 150.59 445.3	PaC, PsN, PsC, PsS, DC, DS, GN, GC, GS.
H. mesophaeum Fr.	Prep.	G	T–2	A–C–e	7	8.84	DN.
H. pumilum Lange	Prep.	G	T–2	B–C–b			GS.
H. strophosum (Fr.) Sacc.	Prep.	G	T–2	B–C–b			DN.
H. testaceum Fr.	Prep.	G	T–2	B–C–b		35.3	DN.
Inocybe agglutinata Pk.	Prev.	G	T–2	B–C–g		18.85 75.07 117.8	PsN, PsS, GN.
I. albodisca Pk.	Prep.	G	T–2	E–C–b		137.5	GS.
I. nr. *bakeri* Smith	Prep.	G	T–2	B–A–b		98.2	DS.
I. castanea Pk.	Prep.	G	T–2	B–C–b		35.3 76.2 117.8	GC.
I. deglubens Fr. *sensu* Singer	Prep.	G	T–2	B–C–e		28.3	PsC.
I. eutheles (Berk. & Br.) Sacc.	Prep.	G	T–2	B–C–b		75.4	DC.
I. fastigiata (Fr.) Quél. v. 22183	Prep.	G	T–2	B–C–e		2479.0	PsS.
I. fastigiata v. 21948	App.	G	T–2	B–C–f		100.5 527.4 954.3	PsS, DC.
I. fastigiata v. *?arenicola* Heim	App.	G	T–2	B–C–f		117.8	PaN, PsS.
I. fastigiata v. *curreyi* (Berk.) Heim	Prep.	G	T–2	C–A–e			PaS.
I. friesii f. *laricina* Heim ap. Bres.	Prev.	G	T–2	B–C–f		35.3 55.22 87.96	PsN, DS, GN.
I. friesii f. *nemorosa* Heim ap. Bres.	Prev.	G	T–2	H–E–f		12.57	PaS, DC.
I. geophylla (Fr.) Quél. v. 21589	Prep.	G	T–2	B–C–b		87.96	PsN.
I. geophylla v. *geophylla*	Prev.	G	T–2	B–C–g		10.6 38.76 78.5	PsN, PsS, DC, GN, GS.
I. geophylla v. *lateritia* Weinm.	Prev.	G	T–2	K–C–g		8.84 62.53 113.1	PsN, PsS, DC, GN, GS.
I. geophylla v. *lateritia* f. *perplexans* Karst.	Prep.	G	T–2	B–C–b		15.7	GN.
I. geophylla v. *lilacina* Fr.	Prev.	G	T–2	B–C–f		42.4 50.7 75.4	PsN, GN, GC.
I. geophylla v. *violacea* Pat.	Prep.	G	T–2	B–C–b		35.3	DC.
I. kaufmannii A. H. Smith	Prep.	G	T–2	B–C–a		38.5	GN.
I. nr. *langei* Heim v. *maior* Singer	Prep.	G	T–2	A–C–e		28.3	GS.
I. nr. *lanuginosa* (Fr.) Bres.	Prep.	G	T–2	B–C–a		50.3	GC
I. obscura (Fr.) Gill. v. 18963	Prep.	G	T–2	A–C–e			DS.
I. obscura v. 24459	Prep.	G	T–2	C–C–a			DC.
I. olympiana A. H. Smith	App.	G	T–2	B–C–d		117.8	DC, GN.
I. pallidipes Ell. & Ev. *sensu* Kauffman	Prev.	G	T–2	B–C–d		9.42 18.25 35.3	DC, GN, GS.
I. pallidobrunnea Kauffman	App.	G	T–2	A–C–f		9.42 18.37 24.5	GS.
I. posterula (Brib.) Sacc.	Prep.	G	T–2	B–C–e		100.5	PsN.
I. radiata Pk.	App.	G	T–2	C–A–e			PaS, DS.
I. nr. *rubens* (Heim) Stuntz	Prep.	G	T–2	B–C–b		18.85	DN.
I. subdestricta Kauffman	Prev.	G	T–2	H–E–f		42.4 74.35 100.5	PsS, DC, GC, GS.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
I. subochracea (Pk.) Earle	Prep.	G	T–2	B–C–b				57.7			GC.
I. trechispora (Berk.) Karst. *sensu* Kauffman	Prev.	G	T–2	B–C–f				12.57			PsN, PsS, GN.
Inocybe 21639	App.	G	T–2	B–C–b				29.5	32.4	35.3	PaN, GN.
Inocybe 22148	App.	G	T–2	B–C–c				75.4			PsS, DC.
Inocybe 22249	Prep.	G	T–2	B–C–c				12.5	43.9	75.4	PaS.
Inocybe sect. *Fricsiae* 25166	Prep.	G	T–2	D–A–b							DS.
Inocybe spp.	?	G	T–2	H–C–g				10.6	77.64	176.7	PaC, PsN, PsC, PsS, DC, DS, GN, GC, GS.
Naucoria sp.	Prep.	G	T–2	A–C–c				7.07			PsS.
Crepidotaceae											
Crepidotus crocophyllus (Berk.) Sacc.	Prep.	W	T–2	B–C–b							DC.
C. nephrodes (B. & C.) Sacc.	App.	L	T–2	B–C–f							DC.
C. sphaerosporus Pat.	Prev.	L	T–2	H–C–g							SN, DC, DS.
C. ?submollis Murr.	Prev.	L	T–2	A–C–f							SN, DS.
C. variabilis (Pers. ex Fr.) Quél.	Prev.	L	T–2	K–C–g							SN, DS, GS.
Ripartites tricholoma (Alb. & Schw.) Karst.	Prep.	G	T–2	A–C–c	3			125.7			PsC.
Tubaria pellucida (Fr.) Gill.	Prev.	G	T–2	A–C–f	2	7	10	1.57	7.3	14.1	SN, PsN, PsS.
Tubaria 18657	Prep.	G	T–2	A–C–b	1	72	304	0.79			PsC.
Tubaria 24537	Prev.	G	T–2	C–C–f	83	96	119	6.28	22.38	42.4	SN, SC, PsC.
Tubaria 20855	Prev.	G	T–2	B–C–g	5	51	184	5.3	18.42	62.8	SN, SC, SS, PsC, DC.
Tubaria 21218	Prev.	G	T–2	B–C–g	3	55	126	19.7	38.8	62 8	FN, FC, SN, SC, PsS.
"*Ochrosporeae*" spp.	?	G	T–2	O–E–g	4	86	649	0.079	14.9	176.7	FN, FC, FS, SN, SC, SS, PaN, PaC, PaS, PsN, PsC, PsS, DN, DC, DS, GN, GC, GS.
Rhodophyllaceae											
Rhodophyllus 19783	App.	G	T–2	B–E–c	3			7.07	9.82	12.57	FC, FS.
Rhodophyllus 19602	App.	G	T–2	B–E–d	15			2.36	2.95	3.53	PaC.
Rhydophyllus 22098A	Prep.	G	T–2	B–C–b	4			20.5			GC.
Rhodophyllus 22089B	Prep.	G	T–2	B–C–b	3			10.6			GC.
Rhodophyllus 21974	App.	G	T–2	B–C–b	1	4	7	38.5	97.8	157.1	PsC, DC.
Rhodophyllus 19782	Prep.	G	T–2	B–A–c	2			21.2			FS.
Rhodophyllus 21827	App.	G	T–2	B–C–b	4	5	6	14.7	17.9	21.2	SC.
Rhodophyllus 21724	Prep.	G	T–2	B–C–b	37			62.8			FN.
Rhodophyllus 19792	Prep.	G	T–2	B–A–c	1			98.2			FS.
Rhodophyllus 24428	Prep.	G	T–2	C–C–a	1			24.54			DC.
Rhodophyllus 20773	Prep.	G	T–2	B–C–a	1			24.54			GN.
Rhodophyllus 21133	Prep.	G	T–2	B–C–a	3			42.4			DC.
Rhodophyllus 21992	Prep.	G	T–2	B–C–b	4			7.07			PaC.
Rhodophyllus 22712	Prep.	G	T–2	B–C–c	4			9.4			FC.
Rhodophyllus 21818	Prep.	G	T–2	B–C–b	10			9.4			FC.
Rhodophyllus 21388	Prep.	G	T–2	B–C–a	1			3.1			FS.
Rhodophyllus 21839	Prep.	G	T–2	B–C–b	2			24.5			SC.
Rhodophyllus 22225	Prep.	G	T–2	B–C–b	1			12.57			SS.
Rhodophyllus 22203	Prev.	G	T–2	B–C–b	5	7	9	19.6	25.4	28.3	FN, FS, SS.
Rhodophyllus 19789	?	G	T–2	H–A–f	4	10	16	7.07	77.76	176.7	FS, SS, PsN, DS.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
Rhodophylleae 19600	App.	G	T–2	B–E–b	2	3	5	3.14	3.64	3.93	SS, PaC.
Rhodophylleae 21738	Prep.	G	T–2	B–C–b	3			9.4			SN.
Rhodophylleae 19570	Prep.	G	T–2	B–A–b	7			19.6			DN.
Rhodophylleae 21197	Prep.	G	T–2	B–C–a	19			35.3			SC.
Rhodophylleae 22722	Prep.	G	T–2	B–C–b	2			21.2			SC.
Rhodophylleae 22684	Prep.	G	T–2	B–C–b	1			35.3			PsC.
Rhodophylleae 21669	Prep.	G	T–2	B–C–b	4			15.7			DN.
Rhodophylleae 20911	Prev.	G	T–2	B–C–e	14	25	36	2.36	11.51	19.6	PaN, PsN, PsC.
Rhodophylleae 22261	Prep.	G	T–2	B–C–e	8			15.7			PaS.
Rhodophylleae 20973	Prep.	G	T–2	B–C–a	1			3.14			PsC.
Rhodophylleae 20801	Prep.	G	T–2	B–C–a	1			35.3			GN.
Rhodophylleae 22723	Prep.	G	T–2	B–C–c	2			137.4			SC.
Rhodophylleae 22227	Prep.	G	T–2	B–C–c	40			14.7			SS.
Rhodophylleae 22790	Prep.	G	T–2	B–C–c	26			75.4			DC.
Rhodophylleae 21780	App.	G	T–2	B–C–b	1	2	3	62.8	69.1	75.4	PaS, PsC.
Rhodophylleae 21749	Prev.	G	T–2	B–C–f	3	6	10	35.3	102.5	269.4	SN, SC, SS, DC.
Paxillaceae											
Hygrophoropsis aurantiaca (Fr.) Maire	Prev.	G	T–2	B–C–d	1	6	16	12.57	65.1	153.9	PsC, PsS, GN.
Paxillus panuoides (Fr. ex Fr.) Fr.	App.	W	T–2	H–E–d	5	7	10	7.95	9.35	9.82	GN.
Gomphidiaceae											
Gomphidius glutinosus Fr.	App.	G	T–2	E–C–d	1	10	27				DN, GS.
G. oregonensis Pk.	Prev.	G	T–2	L–C–d	1	5	9				DN, DS, GC, GS.
G. rutilans (Fr.) Lundell & Nannfeldt	Prev.	G	T–2	B–C–d	1	3	5				PsS, GN.
G. smithii Singer	Prep.	G	T–2	A–C–a	1						GS.
G. subroseus Kauffman v. *subroseus*	Prev.	G	T–2	B–C–d	7	14	27				DN, DC, GN.
G. subroseus v. *homeobasis* Singer	Prep.	G	T–2	B–C–b	4						DC.
Boletaceae											
Boletinus amabilis (Pk.) Snell	Prev.	GM	T–2	I–C–d	43	191	436	47.1	355.8	678.8	DN, DC, DS, GS.
B. cavipes (Opat.) Kalchbr.	Prev.	GM	T–2	B–C–d	20	40	72	35.34	454.1	1413.7	GN, GC.
B. lakei (Murr.) Sing.	Prev.	GM	T–2	H–C–d	15	66	116	47.1	317.8	707.8	DN, DS, GN, GS.
Phylloporus rhodoxanthus ssp. *americanus* Singer	Prep.	G	T–2	B–C–b	2			75.4			GN.
Suiilus grevillei (Klotzsch.) Singer	Prev.	GM	T–2	B–C–d	23	46	70	70.7	465.5	760.3	GN, GC.
S. hirtellus (Pk.) Snell v. *nutans* Pk. in Snell	Prep.	GM	T–2	B–C–b	2	3	5	62.8	370.7	678.6	GN.
S. punctipes (Pk.) Singer	Prev.	GM	T–2	E–C–g	2	103	327	31.4	499.6	1272.4	PaN, PaC, PsN, PsC, PsS, DN, DC, DS, GN, GC.
S. subluteus (Pk.) Snell in Slipp & Snell	Prev.	GM	T–2	B–C–d	4	19	30	62.8	324.1	760.3	DC, GN, GC, GS.
Russulaceae											
Lactarius sanguifluus Fr.	Prev.	G	T–2	O–C–g	1	34	170	95.03	358.9	815.3	PsC, DS, GN, GC, GS.
Lactarius 21919	Prep.	G	T–2	B–C–b	1			5.3			DC.
Russula albidula Pk. ss. Kauffman	App.	G	T–2	A–C–b	2	3	4	50.3	56.9	63.6	GS.
R. borealis Kauffman	Prev.	G	T–2	E–C–e	5	41	84	3.14	361.02	1194.6	PaS, PsN, PsS, GN.
R. delica Fr.	Prev.	G	T–2	H–C–d	1	15	36	7.07	1598.49	6285.2	PsN, DN, GN, GS.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest			Volume of Fruit Bodies Least-Average-Largest			Distribution: Association, Plot
R. palustris Pk.	Prep.	G	T–2	A–C–b	17			98.2			GS.
Russula 21928	Prep.	G	T–2	B–C–b	1			169.6			DC.
Russula 21266	Prev.	G	T–2	B–C–d	2	4	10	117.8	137.8	197.7	GN, GS.
Russula 20839	Prev.	G	T–2	B–C–d	1	18	41	54.98	284.09	502.7	DS, GN, GC, GS.
Russula 20844	App.	G	T–2	B–C–d	1		2	197.6	226.1	254.5	GN.
Russula 22507	Prep.	G	T–2	B–C–b	1			1194.6			GN.
Russula 20840	Prev.	G	T–2	B–C–d	1	6	11	75.4	138.3	230.9	DS, GN, GS.
Russula 19808	App.	G	T–2	B–E–f	1		2	16.64	47.57	78.5	PsS.
Russula 20841	App.	G	T–2	B–C–f	10			141.4	579.7	1017.9	PsS, GN.
Russula 20842	Prev.	G	T–2	B–C–d	1	11	32	35.3	129.53	351.9	DC, GN, GC, GS.
Russula 21526	Prev.	G	T–2	B–C–d	3	7	9	75.4	478.4	1327.3	PsN, PsS, GN, GC, GS.
Russula 24370	?	G	T–2	C–C–d	1	11	23	35.3	145.98	552.9	DS, GN, GC, GS.
Russula 18606	Prep.	G	T–2	A–C–b							GS.
Gasteromycetes											
Lycoperdales											
Lycoperdaceae											
Bovista pila Berk. & Curt.	Prep.	G	T–4	B–C–a	3			6.28			SS.
B. plumbea Pers.	Prev.	G	T–4	I–E–g	1	3	5	2.65			FC, FS, SN, SS, DC.
Bovistella radicata (Dur. & Mont.) Pat.	App.	G	T–4	H–E–f	1	2	3	2.65	5.07	6.28	FN, FS, SS.
Calvatia craniiformis (Schw.) Fr.	Prep.	G	T–4	B–C–b	1			309.7			PaC.
Lycoperdon sp.	Prep.	G	T–4	H–E–b	1		2	2.65			FN, PaC.
L. perlatum Pers.	Prev.	G	T–4	O–C–g	1	9	22	9.4			FC, PaC, PaS, PsN, PsS, DN, DC, DS, GN, GC, GS.
L. pusillum Pers.	Prev.	G	T–4	H–E–f	2	2	3	2.65			FN, FS, PsS.
L. rimulatum Pk. ex Trelease	App.	G	T–4	B–E–e	1	2	3	2.65			PaS, DN.
L. marginatum Vitt.	Prev.	G	T–4	K–E–g	1	8	31	2.65			PaS, DC, DS, GC, GS.
L. umbrinum Pers.	Prev.	G	T–4	O–E–g	1	3	6	2.65			FN, FS, SS, DN, GC.
Geastraceae											
Geastrum minus (Pers.) Cunn.	App.	G	T–4	L–E–g	1	10	27	1.57	1.96	3.14	PaS, DN, DC, GS.
G. rufescens Pers.	App.	G	T–4	O–E–g	1	4	6	18.85	20.7	28.3	SS, DN, GS.
Sclerodermatales											
Sclerodermataceae											
Scleroderma cepa (Vaill.) Pers.	Prep.	G	T–4	A–C–c	2			75.4			DN.
Nidulariales											
Nidulariaceae											
Crucibulum levis (DC.) Kambly	Prev.	W	T–4	O–C–g							DN, GN, GC.
Cyathus stercoreus (Schw.) DeToni	App.	D	T–4	B–C–d							PaS.
Hymenogastrales											
Hymenogastraceae											
Hymenogaster ?remyi Zeller & Dodge	Prep.	H	T–4	B–A–c							GN.
Hydnangiaceae											
Hydnangium sp.	Prep.	H	T–4	B–C–a							PaN, GN.
H. darkeri Zeller	Prep.	H	T–4	C–C–b							GN.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average-Largest	Volume of Fruit Bodies Least-Average-Largest	Distribution: Association, Plot
Fungi Imperfecti							
Phomales							
Phomaceae							
Ascochyta lomatiae W. B. Cke.	App.	P	L	C–A–b			FC, SC.
Asteroma tenerrimum v. *erythronii* Sacc.	App.	P	L	H–A–f			SC, PaS, DS.
Cytospora globifera Fr.	Prep.	P	W	A–C–c			DS.
Phyllosticta fritillariae Bonar & W. B. Cke.	App.	P	L	C–A–c			FC, SS.
P. vagans Pk.	Prep.	P	L	B–A–c			DS.
Phyllosticta sp.	Prep.	P	L	C–C–a			DS.
Septoria coptidis Berk. & Curt.	Prep.	P	L	C–A–b			GC.
S. symphoricarpi Ell. & Ev.	Prev.	P	L	J–D–e			FC, SC, SS, PaS, DC.
S. rhoina Berk. & Curt.	Prep.	P	L	J–F–a			PaS.
Melanconiales							
Melanconiaceae							
Dinemasporium graminum Lév.	Prep.	P	L	D–A–a			DS.
Hainsia borealis Ell. & Ev.	App.	P	L	D–B–a			FS, SS.
Marssonina potentillae (Desm.) Magn.	Prep.	P	L	C–A–c			SC.
M. wyethiae (Ell. & Ev.) Magn.	Prep.	P	L	J–A–f			FC.
Titaeospora detospora Bub.	Prep.	P	L	D–B–a			FS.
Vermicularia liliacearum Westd.	Prep.	P	L	J–A–b			SS.
Moniliales							
Moniliaceae							
Aspergillus flavus Lk.	App.	S	M	C–A–b			FC, PaS.
A. fumigatus Fres.	Prep.	S	M	C–A–b			PaC.
A. niger van Tieghem	Prev.	S	M	C–A–b			FC, SS, PaS, DN, GC, GS.
Geotrichum candidum (Lk.) Pers.	Prep.	S	M	C–A–b			FC.
Monosporium agaricinum Bon.	Prep.	F	M	B–C–a			GC.
Mycogone rosea Lk.	App.	F	M	B–C–f			PsN, DS.
Oidium (*sensu* Linder) sp.	Prep.	W	M	A–C–c			PaS.
Ovularia pusilla (Ung.) Sacc.	Prep.	P	L	C–C–a			PaS.
Penicillium canescens Sopp	Prep.	S	M	C–A–b			DC.
P. crustosum Thom	Prep.	S	M	C–A–b			DC.
P. decumbens Thom	Prev.	S	M	C–A–b			SN, SC, PaC, PsN, DS.
P. diversum v. *aureum* Raper & Fennell	Prep.	S	M	C–A–b			PsN.
P. frequentens Westling	Prep.	S	M	C–A–b			PsN.
P. fuscum (Sopp) Raper	Prep.	S	M	C–A–b			GS.
P. kapuscinskii Zaleski	Prev.	S	M	C–A–b			PaS, PsN, PsC, PsS, DN, DC, DS, GC, GS.
P. lanosum Westling	Prep.	S	M	C–A–b			FC.
P. martensii Biourge	Prep.	S	M	C–A–b			FN.
P. nigricans (Bainier) Thom	Prev.	S	M	C–A–b			PaN, PaS, PsC.
P. piscarium Westling	Prep.	S	M	C–A–b			PaS.
P. purpurascens (Sopp) Raper	Prep.	S	M	C–A–b			FN.
P. raciborskii Zaleski	Prev.	S	M	C–A–b			FN, FC, FS, SN, SS, PaN, DC, GS.
P. raistrickii Smith	Prep.	S	M	C–A–b			PsS.
P. restricium Gilman & Abbott	App.	S	M	C–A–b			FC, DC.

TABLE 4B. Continued

Species	Ecologic Status	Habitat	Habit	Year-Season-Trip Classes	Number of Fruit Bodies Least-Average Largest	Volume of Fruit Bodies Least-Average-Largest	Distribution: Association, Plot
P. rugulosum Thom	Prep.	S	M	C–A–b			PaS.
P. simplicissimum Sacc.	Prep.	S	M	C–A–b			FC.
P. spinulosum Thom	Prev.	S	M	C–A–b			FC, SN, SS, PaS, PsN, DC, DN, GN.
P. thomii Maire	Prev.	S	M	C–A–b			FN, FS, SS, PaN, PsS, DS.
P. viridicatum Westling	Prep.	S	M	C–A–b			SC.
Penicillium sp. (Brevi-compactum series)	Prep.	S	M	C–A–b			PsS.
Ramularia arvensis Sacc.	Prep.	P	L	D–B–a			SS.
R. cercosporioides Ell. & Ev.	Prep.	P	L	D–B–a			FS.
R. cynariae Sacc.	App.	P	L	J–D–e			FC, FS, PsS.
R. heraclei (Oud.) Sacc.	App.	P	L	C–A–b			FC, SC.
R. nivosa (Ell. & Ev.) W. B. Cke. & Shaw	Prep.	P	L	C–A–e			DS.
R. philadelphi Sacc.	Prep.	P	L	C–A–e			DS.
R. smilacinae J. J. Davis	Prep.	P	L	D–A–b			DS.
Scopulariopsis brevicaulis Bainier	Prep.	S	M	C–A–b			PsN.
Spicaria violacea Harz	Prep.	S	M	C–A–b			SN.
Trichoderma viride Fr.	Prev.	S, W	M	H–E–d			FN, FC, FS, SC, SS, PaC, PaS, PsN, DN, DC, GN.
Dematiaceae							
Cladosporium epimyces Cke.	Prep.	F	M	C–C–a			DN.
Haplographium bicolor Grove	Prev.	S	M	C–A–b			PaN, PsN, GS.
Helminthosporium acroleucum Sacc., Bomm & Rouss.	Prep.	W	M	C–A–e			DS.
H. pseudotsugae W. B. Cke.	Prev.	W	M	O–E–g			DC, DS, GN, GC, GS.
Heterosporium allii v. *sisyrinchii* Speg.	Prep.	P	L	C–A–e			FC.
H. gracile (Wallr.) Sacc.	Prep.	P	L	D–A–b			SS.
Hormodendrum viride (Fres.) Sacc.	App.	S	M	C–A–b			SS, GC.
Macrosporium commune Rab.	Prep.	S	M	C–A–b			DC.
Macrosporium iridis Cke. & Ell.	App.	P	L	C–A–e			FC, SS.
Papularia sphaerosperma (Pers.) V. Hoehn.	Prep.	S	M	C–A–b			PsC.
Pullularia pullulans (deBary) Berkhout	Prep.	S	M	C–A–b			FC.
Stachylidium extorre Sacc.	Prep.	S	M	C–A–b			GS.
Stemphyllium consortiale (Thuem.) Groves & Skolko	App.	S	M	C–A–b			FC, SC.
Tuberculariaceae							
Stromatocrea cerebella W. B. Cke.	App.	W	T–5	H–E–e			DC, GN.
Exosporium pedunculatum (Ell. & Ev.) W. B. Cke.	Prep.	W	T–5	D–B–a			PaN.
Fusarium spp.	App.	S	M	C–A–b			SS, GC.
Pestalotia virgulata Klebahn	Prep.	S	M	C–A–b			FC.
Tuberculariа sp.	Prep.	W	T–5	C–A–b			SS.
Stilbaceae							
Isaria sp.	Prep.	S	M	A–C–b			FS.
Dermatophytes							
Microsporum gypseum (Bodin) Gniart & Grigorakis	Prev.	SC	M	D–A–e			SC, SS, PaS.
Mycelia Sterilia							
Papulospora sp.	Prep.	S	M	C–A–b			SS.

TABLE 5. Comparison of Fungus Activity

Plot	Degradation: Percentage Loss of Tensility		Plate Count: Colonies per Gram Soil (Dilution—1:1000)	Total Macromycete Fruit Bodies Observed 1946-1949
	Cotton	Wool		
FN	57.8	15.6	32,750	1,224
FC	56.5	15.6	39,250	96
FS	70.8	42.2	51,000	906
SN	94.4	32.1	50,000	1,323
SC	70.1	100.0	8,750	2,356
SS	74.5	35.8	94,250	257
PaN	14.5	10.1	274,000	3,378
PaC	....*	....*	42,000	2,639
PaS	95.1	50.7	71,750	1,935
PsN	46.2	23.3	183,000	6,297
PsC	35.5	....†	50,250	3,305
PsS	55.9	9.2	131,250	1,447
DN	21.6	11.9	339,250	30,757
DC	34.3	17.4	80,000	19,186
DS	71.9	65.2	67,250	3,807
GN	24.9	11.1	102,500	149,146
GC	9.4	10.2	40,500	36,008
GS	....*	....*	127,250	3,208

*Not tested.
†Strips removed by rodents.

Results of preliminary studies on microbiological activities in the plots present little material on which to base a correlation within or among associations. More than one series of isolations would be necessary to present an adequate idea of the speciation of the populations in the soil and such isolations would have to be carried out with various differential media as indicated by the experiment in which cotton and wool cloths were used. Differences among plate counts based on one series of isolations can possibly be explained on the basis of sampling techniques, which could be improved by better selection of sites from which to obtain composite samples, and organic matter content of the soil which varies in quantity and quality on various parts of each plot.

CONSTANCY

Fungi.—The 815 species of fungi (including micro- and macro-mycetes) reported in this paper are distributed throughout the six associations studied according to table 4. Their distribution within the stands of each association is summarized in table 6.

The data suggest a relatively low degree of constancy for the fungi, but there is a tendency toward increasing constancy in the more moist associations. (Constancy refers to the occurrence of species in large sample areas of uniform size located in different stands over the geographic range of an association.) The latter is all the more significant for the fact that it accompanies an increase in richness of the fungus flora. This increasing constancy tends to confirm the observations of other mycologists that there is a high degree of ubiquity expressed in the fungi. In fact, throughout the groups of fungi studied, there are a number of species which have been reported from all the continents of the northern hemisphere and from some of those in the southern hemisphere. Even correcting for misidentification there are a comparatively large number of species of fungi which have world-wide or near world-wide distribution.

TABLE 6. Constancy

Association	Number of Species Observed	Percentage of Grand Total of Species	Percentage of Species		
			In One Plot	In Two Plots Only	In Three Plots
			Fungi		
F.....	108	13	74.1	18.5	7.4
S.....	168	20.5	72.6	20.7	6.5
Pa.....	203	30	74.0	20.7	5.3
Ps.....	287	36	71.6	19.5	9.6
D.....	345	44	75.0	16.7	8.3
G.....	367	44.5	66.1	23.2	10.7
Total...	815				
			Lichens		
F.....	7	4.9	71.4	14.3	14.3
S.....	5	3.5	100.0	0	0
Pa.....	48	33.7	79.1	12.4	8.3
Ps.....	55	38.7	78.2	16.4	5.5
D.....	68	47.5	75.0	20.6	4.4
G.....	41	28.8	65.8	27.0	6.2
Total...	142				
			Bryophytes		
F.....	13	16.5	69.2	23.1	7.7
S.....	9	11.4	77.8	0	22.2
Pa.....	11	13.9	81.8	18.2	0
Ps.....	30	38.0	73.3	20.0	6.7
D.....	47	58.5	76.6	17.0	6.4
G.....	24	30.4	71.0	25.0	4.0
Total...	79				

Lichens.—Table 4 lists the species and their distribution, and table 6 indicates the percentage of species of lichens found in one, two or three plots of each of the six associations. This table indicates highest constancy in the *Symphoricarpos/Festuca* association where all species collected were found on branches on the shrubs. All species in the impoverished lichen biota of the *Festuca/Agropyron* association grow on the ground. No clearly defined gradient in constancy is apparent in this group of species.

Bryophytes.—Table 4 lists the species and their distribution, while table 6 indicates the percentage of species of Bryophytes found in one, two and three plots of each of the six associations. This table indicates that a greater number of species occur in all three plots in the *Spmphoricarpos/Festuca* association but because of the paucity of species this conclusion may not be valid. Also, apparently a greater number of species occurs in all three plots of an association in the lower elevations.

FIDELITY

Differences in fungus populations among the six associations were not well expressed by parasitic fungi since these were restricted to the hosts which they parasitize. Where the host plant occurs in more than one plot or in more than one association the parasite may usually be found with it. Thus *Cumminsiella mirabilissima* (Pk.) Nannf. was found wherever its host *Berberis repens* Lindl. was found, but *Puccinia crandallii* Pam. & Hume was found occasionally with its aecial host *Symphoricarpos albus* and its telial host *Festuca idahoensis*, and then not in every observation year.

Likewise, differences between the fungus activities of the six associations were not well expressed by fungi saprobic (living on dead organic matter) on rotten wood and herbaceous litter. Certain fungi restricted to conifer wood were not always found with conifer wood and the same was true of herbaceous litter and wood of broad-leaved plants.

The most significant differences among the plots are shown (table 7) by the larger fleshy fungi usually referred to as mushrooms or toadstools. This may be a response to differences in nutritional requirements, mycorrhizal host specificity, availability of moisture in the fruiting season, or other factors in the biology of the fungi not yet apparent. It is also possible that a larger number of species is widely distributed in the lower zones but are not able to reach a stage in which fruit bodies can be produced because their growth period is shortened by cold winters and dry summers.

The number of species in contiguous associations which appear not to cross the ecotone between these associations is taken as a criterion of fidelity. (Fidelity is defined as the degree to which a species is confined to a community or an association.)

TABLE 7. Fidelity: Ecotone Relationship

Ecotone	Percent of Species in Contiguous Associations Which Appear not to Cross the Ecotone		
	Fungi	*Lichens*	*Bryophytes*
F–S	79.0	92.8	76.2
F–Pa	87.8	92.9	91.7
S–Pa	87.2	100.0	89.1
S–Ps	86.8	95.0	86.5
Pa–Ps	81.0	87.4	90.0
Ps–D	77.7	81.6	78.4
D–G	74.8	80.0	79.1

Lichens appear to show a greater degree of fidelity than fungi or bryophytes which may be a reflection of fewer types or available substratum for these unions and of dryer micro-habitats.

It is to be noted that the conspicuous break in vascular floras between the *Pseudotsuga taxifolia/Physocarpus* and *Ablies grandis/Pachistima* associations (Daubenmire 1952), finds no counterpart in the cryptogamic biotas.

A second method of expression of the fidelity of the species of organisms studied is shown by a series of histograms based on the percentage of organisms of one association that are found in each of the other associations. In figure 7 (fungi), figure 8 (lichens) and figure 9 (bryophytes) each horizontal array represents the species found in one association. Each column represents the percentage of species based on the tallest column taken as 100%.

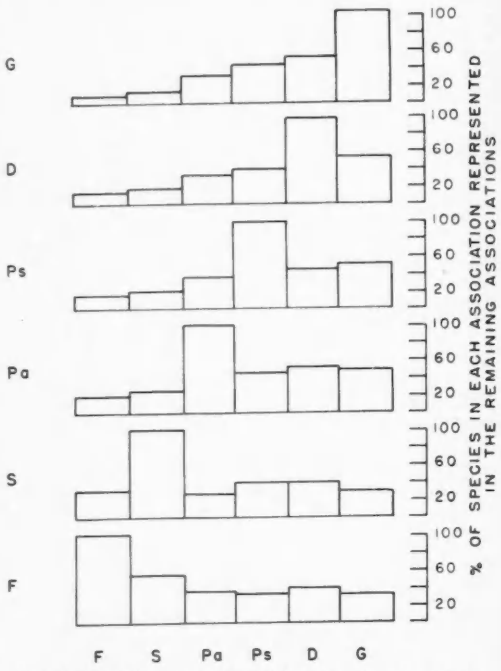

FIG. 7. Fidelity: Percent of Fungi in One Association Found in Contiguous Associations.

From this analysis it may be concluded that there is a general tendency toward more distinctive biotas in the direction of more mesophytism, especially when considering the central group of associations. This may simply reflect the increasing richness of the fungus populations in progressing upward through the series of associations. Essentially the same conclusions may be drawn for lichens and bryophytes.

VIGOR

Vitality classes as used in studies with higher plants are for the most part not applicable in myco-sociology. A class of species which fruit weakly may be recognized as consistently being represented by only one to a few fruit bodies and being collected on only one visit to a plot. All other species could be represented by a second class in which the species fruit comparatively vigorously. The existence of a class which reproduces only vegetatively may be suspected, but no real evidence can be offered unless members of the Fungi Imperfecti which fruit only asexually are placed here.

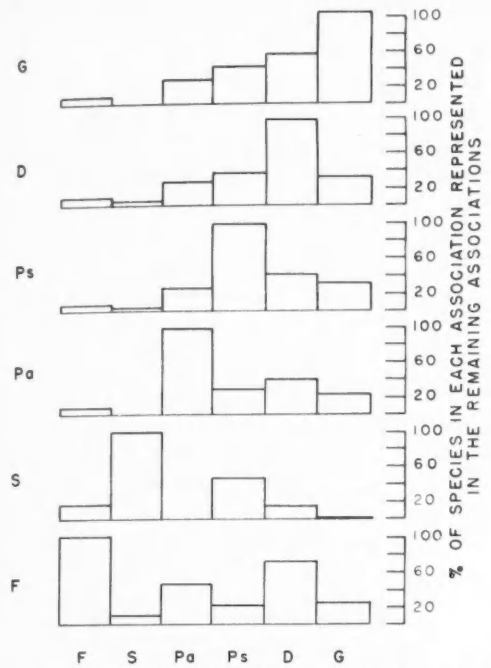

FIG. 8. Fidelity: Percent of Lichens in One Association found in Contiguous Associations.

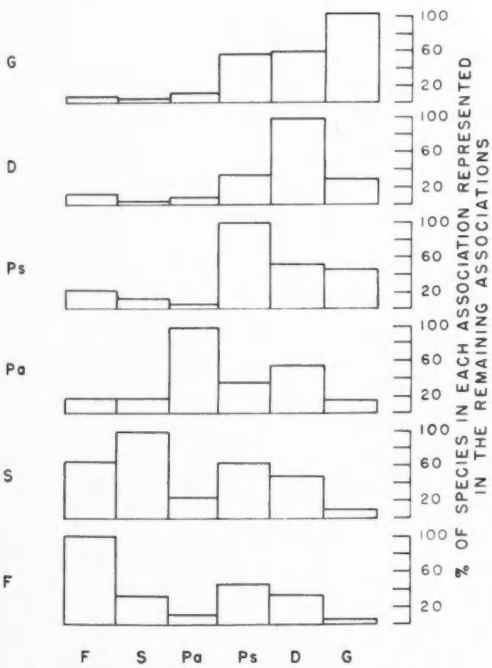

FIG. 9. Fidelity: Percent of Bryophytes in One Association Found in Contiguous Associations.

Most species collected in the fall of 1947 displayed exceptional vigor, possibly because the rains started early in September and continued throughout the collecting season. In the other fall seasons rain did not occur so generally nor in such large amounts so that if fruit body production got a good start it may have been held back by periods of desiccation between rainfalls or by early snows. Those species which fruited in all fall seasons appear to have had smaller fruit bodies in 1946, 1948 and 1949 than in 1947. Spring fruiting generally resulted in smaller fruit bodies than fall when the species appeared in both seasons. Early season fruit bodies were generally smaller than late season fruit bodies of the same species.

DOMINANCE

A numerical basis for dominance was obtained from the formula: Pi times radius of sporophore squared times height times number of fruit bodies. (Dominance is defined as the relative size or bulk of the shoots of each species expressed quantitatively in conjunction with area.) Values used for calculation of this figure were based on average diameter of caps and average height of fruit bodies based on length of stipe from soil to bottom of pileus. A summary of the total volume occupied by the counted or estimated total fruit bodies of each genus is presented in table 8. For each species these figures usually vary from season to season, from plot to plot, from date to date in the same plot, and in the same plot from one more or less similar habitat to another. A very few species, less than 1% of the total list, have fruit bodies clustered in large masses from a single center of growth. In the case of these fasciculate species the volume value gives little idea of the space occupied by the fruit bodies of a species on the plot. Since these fungi are represented to the collector only by their fruit bodies the volume value cannot give an idea of the extent to which an individual mycelium is distributed in the substratum. Thus dominance here has physiognomic rather than competitive significance.

Many species occupy mutually exclusive habitats. Some grow only on cones, others only on rotten wood; some fruit in openings, others in the denser parts of the forest, some with particular trees, others apparently without regard to the forest constituents. Judging from the level of the base of the stipe there seem to be several layers of mycelial activity in the ground from fungi growing principally in the surface litter layers to those in the duff, and still others in the mineral soil beneath the duff. It is possible that several mycelia may occupy the same general space in the same layer of litter, duff or soil.

From the fact that fungi fruit in many different microhabitats above ground and that there may have been several unions of fungus mycelium underground, any estimate of dominance of epigaeous or hypogaeous fruit bodies as a single category can only be superficial.

SOCIABILITY

Sociability of fruit bodies within a species of fungus is probably concerned for the most part with the

TABLE 8. Total Dominance of Fungi by Genera

Genus	Associations											
	F		S		Pa		Ps		D		G	
	Number Fruit Bodies	Volume in cc.	Number Fruit Bodies	Volume in cc.	Number Fruit Bodies	Volume in cc	Number Fruit Bodies	Volume in cc	Number Fruit Bodies	Volume in cc	Number Fruit Bodies	Volume in cc
Bovistella	2	9	3	19								
Stropharia	10	373	9	344	9	372	14	629				
Psilocybe	12	168					10	32				
Coprinus	15	41	3	144	6	44			7	746		
Pleurotus	71	38					10	102	20	32		
Panaeolus	14	845	52	2,216	73	6,005	18	1,283	35	2,772		
Tubaria	87	1,845	1,429	30,858			214	7,533	9	191		
Bovista	5	13	8	33					2	6		
Mycena	311	9,219	631	16,988	2,627	23,723	2,710	39,186	6,444	119,780	9,002	197,590
Marasmius	465	322	108	29	556	4,186	414	6,631	55,018	46,992	280,508	147,574
Hygrophorus	30	1,597	9	516	662	172,859	189	75,481	755	539,003	337	121,799
Cortinarius			23	1,472	818	136,544	741	439,115	1,458	115,783	2,180	336,361
Clavaria (sens. lat.)	2	71			23	279	1,182	35,245	390	2,265	1,843	16,379
Tricholoma	33	9,532	41	9,467	303	35,788	231	182,947	1,374	67,593	195	24,338
Collybia	187	17,056	20	211	80	2,209	1,189	11,176	2,546	34,708	1,286	15,204
Clitocybe	45	13,069	87	5,129	726	20,360	2,531	57,246	1,618	16,685	1,254	16,685
Lepiota	1	28	49	1,455	28	287	6	1,174	136	16,631	26	2,400
Galerina	121	348	577	5,165	102	964	754	8,419	232	2,387	181	1,884
Agaries (undet.)	21	286	131	338	97	585	53	6,862	76	1,304	379	9,644
Lyophyllum	14	550	34	1,782	9	314	7	276	9	217	27	588
Lycoperdon	11	32	7	19	43	298	7	30	53	242	74	446
Xeromphalina	3	7	1,108	10,438			15	469	1,954	24,324	536	7,256
Brown agaric (undet.)	91	783			83	486	49	1,059	1,169	7,219	41	808
Rhodophyllus	61	2,748	25	540	15	35	16	2,827	19	2,358	7	160
Omphalina	51	1,083	3	142	59	155	69	831			32	83
Agaricus	1	21							14	2,099	1	39
Conocybe	9	7	8	32	1	16	4	4				
Dark agaric			4	80								
Lentinus			2	1					42	1,830		
Psathyrella			97	11,000	17	2,274	2	38	54	18,810		
Cystoderma			1	13	101	6,788	344	31,994	436	37,127	321	37,140
Geastrum			1	28					33	52	9	120
Pink agaric (undet.)			52	7,653	52	870	3	171	12	275	1	35
Calvatia					1	308						
Suillus					842	561,282	107	94,172	17	9,095	150	65,583
Coltricia					4	8					13	130
Auriscalpium					14	308	241	5,028	38	836	6	132
Hebeloma					4	1,126	23	3,282	493	58,894	427	73,432
Thelephora					4	443	10	94	2	42	8	52
Inocybe					50	5,464	185	19,320	1,012	147,342	374	23,799
Russula					189	67,979	204	423,624	51	193,238	255	174,713
Armillaria					21	22,599			55	67,449	115	45,419
Amanitopsis					51	39,615					2	4,092
Pholiota					7	825	1	63	10	85	71	7,333
Kuehneromyces					3	593	3	593			8	409
Ripartites							3	3,177				
Pluteus							2	314	3	503		
Helvella							5	895	70	28,264	45	9,219
Clavariadelphus							2	432	56	792	53	2,860
Naematoloma							95	58,658			5	982
Cantharellus							7	351			2	32
Lactarius							1	318	29	12,474	203	115,637
Otidea							105	1,379	788	18,921	50	307

Genus	Associations											
	F		S		Pa		Ps		D		G	
	Number Fruit Bodies	Volume in cc.	Number Fruit Bodies	Volume in cc.	Number Fruit Bodies	Volume in cc	Number Fruit Bodies	Volume in cc	Number Fruit Bodies	Volume in cc	Number Fruit Bodies	Volume in cc
Galerina							12	151			2	18
Polyporus							2	1,257	22	1,674	18	720
Gomphidius							4	2,077	85	17,531	48	19,187
Scleroderma									2	151		
Amanita									2	451		
Morchella									3	57		
Discina									2	101		
Boletinus									654	385,905	350	162,559
Mitrula									576	280	638	195
Flammula									7	247	118	4,731
Spathularia									76	120	459	715
Pseudohydnum									42	396	166	1,635
Laccaria									44	9,980	528	90,373
Pseudoplectania									11	7	50	337
Phlogiotis									3	47	22	198
Phaeolus									1	9,896	2	21,206
Dentinum											21	2,829
Phylloporus											2	151
Calocera											3	1
Totals	1,673	60,091	4,522	106,212	7,610	1,115,961	11,894	1,525,945	77,068	1,996,199	302,414	1,765,419

question of whether more than one mycelium may be responsible for the fruit bodies present in the plot. The determination of the number of mycelial mats in an area can only be estimated since it is not yet feasible to study the mycelium itself. Finding several groups of fruit bodies, each with a somewhat different average volume, at a single visit to the plot probably indicates that more than one mycelium of a species is present in the plot.

Phenology

A phenologic analysis of the field notes at the termination of field studies was made to determine the extent to which the appearance of fruit bodies of each species is confined to a definite season. Table 8 presents a summary of the percentage of fungi fruiting in each plot and association in each season or combination of seasons.

For the most part the spring and fall fungus populations are different. Only about 10% of the species fruit in both spring and fall. From table 9 it is evident that in the altitudinally lower, grassland, plots almost as many species fruit in the spring as in the fall while in the higher plots progressively more species fruit in the fall than in the spring until in the most mesophytic association, the *Abies grandis/Pachistima* association, 73% of the species fruit in the fall only.

Table 10 indicates the percentage of species of fungi collected in the associations under study in relation to the years in which they were found. This indicates that, at least in 1947, fewer species of fungi were restricted to fruiting in the more mesophytic associations in a wet year. In other words, the impoverished fungus flora of xerophytic associations is in large measure a consequence of inadequate moisture to alloy fruiting.

There has been insufficient general work on fungus sociology in North America against which to draw comparisons with the above studies. Such reports as those of Graham (1927), Williams (1936) and Slipp (1944) were largely, if not entirely, qualitative, while work done by Baxter and other forest pathologists was restricted to special groups and special aspects of the occurrence of these groups.

Additional Observations on Lichens

One hundred and fifty-eight species of lichens were obtained in the collections made from the plots. In relating these to the site in which they grew it was necessary to consider a number of habitat factors. The species are listed in table 4A according to their occurrence and habitat in the plots. Some of the species grow on rocks, others on soil, others on rotten wood and some among mosses. Some species grow on rough or smooth bark of *Pinus ponderosa, Pesudotsuga taxifolia* var. *glauca, Abies grandis, Larix occidentalis* and *Pinus contorta* var. *latifolia,* as well as on the bark of branches and twigs in the canopy whether these were living or dead. Another group of species grew on the smooth bark of the trunks of Crataegus, Amelanchier, Salix and Acer, or on the smooth bark of such low shrubs as Rosa and Sym-

TABLE 9. Phenologic Data for Fungi. Percentages of Species Appearing at Different Seasons.

Plot	Species Totals	Fall Only	Spring Only	Spring and Fall	Summer Only	Summer and Fall	Summer and Spring	Summer Fall and Spring
	Percentages of Plot and Association Totals							
FN	46	65.2	28.3	4.3	2.2	0	0	0
FC	52	40.4	42.3	3.8	11.5	0	1.9	0
FS	46	41.3	41.3	10.9	6.5	0	0	0
Total	108	43.4	35.2	13.0	9.3	0	0.9	0
SN	62	66.1	22.6	9.7	1.6	0	0	0
SC	85	63.5	27.1	7.1	0	0	0	1.2
SS	73	58.9	27.4	4.1	4.1	0	4.1	1.4
Total	170	58.8	28.2	8.2	2.4	0	1.8	1.2
PaN	82	78.0	13.4	7.3	2.4	0	0	0
PaC	84	71.4	20.2	7.1	0	0	0	0
PaS	107	63.6	22.4	9.3	1.9	0.9	1.9	0
Total	215	65.6	20.0	12.6	1.4	0.46	0.93	0
PsN	166	76.5	14.5	5.4	0	2.4	1.2	0
PsC	137	75.9	16.8	5.8	0.73	0	0	0
PsS	92	69.6	19.6	8.7	2.2	0	0	0
Total	297	69.8	19.5	9.4	0.34	1.4	1.0	0
DN	129	79.8	12.4	7.8	0	0	0	0
DC	192	80.2	9.4	9.9	0.52	0.52	0.52	0
DS	166	56.6	23.5	17.5	1.2	0	1.2	0
Total	364	72.0	16.2	12.4	0.82	0.27	0.82	0
GN	232	81.9	11.2	6.9	0	0	0	0
GC	166	78.9	15.1	7.2	1.2	0	0	0
GS	150	74.0	16.0	8.7	1.3	0	0	0
Total	370	73.0	14.9	11.1	1.1	0	0	0

TABLE 10. Percent Species of Fungi Collected in One or More Years of the Study.

Association	Percentage of Total Species in all Stands Collected in:							
	1946	1947	1948	1946, 1947	1946, 1947, 1948	1947, 1948	1946, 1948	Total
F	9.6	87.6	2.8	...	...	...	...	100.0
S	8.5	78.1	8.2	3.4	...	0.9	0.9	100.0
Pa	10.3	72.8	5.5	4.8	3.6	3.0	...	100.0
Ps	7.3	72.8	5.1	3.8	4.0	5.9	1.1	100.0
D	10.3	59.8	8.3	5.7	5.1	9.9	0.9	100.0
G	10.9	65.4	5.4	4.3	4.3	9.3	0.5	100.0

phoricarpos and of twigs of shrubs like Crataegus and Amelanchier.

The groups of lichens collected in some of the communities contain species found in other lichen communities. Since no quantitative sociologic data were obtained the relative importance of a species in more than one community cannot be indicated. However, the appearance of a species in several types of habitat may be taken to indicate a wide ecologic amplitude. Lichen communities are listed in table 11.

TABLE 11. Communities of Lichens and Bryophytes. Lichen and bryophyte communities were classified according to fruticose, foliose or crustose lichens, or bryophytes occurring on soil, rotting wood or bark, bark of living trees or shrubs, and stones. No attempt was made to classify these communities in associations because no quantitative data were taken on the species and specimens collected. It is possible that in some of the habitats listed below, the bryophytes played a more important role than the lichens and vice versa but the communities of each type are listed separately.

Lichen Communities

Festuca/Symphoricarpos Association
- On soil
  - Northern and Southern Plots
    - *Peltigera-Cladonia* Community
  - Central Plot
    - *Peltigera-Cladonia-Diploschistes* Community

Symphoricarpos/Festuca Association
- On soil
  - Central Plot
    - *Peltigera* Community
- On canes of *Rosa* spp.
  - Northern Plot
    - *Physcia-Xanthoria* Community
  - Southern Plot
    - *Rinodina* Community
- On branches of *Symphoricarpos, Crataegus, Rosa* and *Amelanchier*
  - Central Plot
    - *Parmelia-Candelaria* Community

Pinus ponderosa/Agropyron Association
- On soil
  - Northern and Southern Plots
    - *Peltigera-Cladonia* Community
  - Central Plot
    - *Cladonia* Community
- On granitic rocks
  - Central Plot
    - *Umbilicaria-Parmelia* Community
    - *Diploschistes-Lecanora-Lecidea-Rhizocarpon-Crocynia* Community
- On basalt rocks
  - Southern Plot
    - *Cladonia* Community
    - *Umbilicaria-Parmelia* Community
    - *Diploschistes-Lecanora-Lecidea-Rhizocarpon-Buellia* Community
- On rotten wood
  - Southern Plot
    - *Cladonia* Community
- On or among mosses
  - Southern Plot
    - *Leptogium* Community
- On branches in the crown of *Pinus ponderosa*
  - All plots
    - *Parmelia-Cetraria* Community
  - Northern and Central Plots
    - *Alectoria-Letharia* Community
  - Southern Plot
    - *Alectoria-Letharia-Usnea* Community
  - Central Plot
    - *Buellia* Community

Pinus ponderosa/Symphoricarpos Association
- On soil
  - All plots
    - *Peltigera-Cladonia* Community
- On rotten wood
  - Northern Plot
    - *Cladonia* Community
  - Southern Plot
    - *Cladonia-Peltigera* Community
    - *Parmeliopsis-Lecidea-Lecanora* Community
- On smooth trunk bark of *Crataegus*
  - Northern Plot
    - *Candelaria-Crocynia-Lecanora-Lecidea-Physcia* Community
- On smooth trunk bark of *Amelanchier* and *Salix*
  - Southern Plot
    - *Parmelia* Community
    - *Buellia-Caloplaca-Candelaria-Candelariella-Lecanora-Physcia-Rinodina-Xanthoria* Community
- On bark of branches and twigs in the crown of *Pinus ponderosa*
  - All plots
    - *Parmelia-Cetraria* Community
  - Northern and Southern Plots
    - *Alectoria-Letharia* Community
  - Central Plot
    - *Letharia* Community
  - Northern Plot
    - *Lecidea* Community
  - Central Plot
    - *Xanthoria* Community
  - Southern Plot
    - *Lecanora-Bacidia* Community

Pseudotsuga/Physocarpus Association
On soil
Northern and Southern Plots
Peltigera-Cladonia Community
On rocks
Northern Plot
Cladonia Community
Southern Plot
Cladonia Community
Peltigera-Parmelia-Lobaria Community
Candelariella-Lecanora-Physcia-Rhizocarpon-Rinodina-Xanthoria Community
On rotten conifer wood
Central and Southern Plots
Cladonia Community
On rotten wood of *Acer*
Northern Plot
Cladonia Community
On or among mosses
Southern Plot
Leptogium Community
On rough bark of *Philadelphus*
Southern Plot
Peltigera-Nephroma Community
On sterile lichen thalli on smooth bark of *Crataegus*
Southern Plot
Buellia Community
On smooth bark of *Acer*
Central Plot
Parmelia Community
Lecanora-Lecidea-Physcia-Rinodina-Xanthoria Community
On stump of *Pseudotsuga*
Southern Plot
Parmeliopsis Community
On rough bark at base of *Pseudotsuga*
Southern Plot
Cladonia Community
On rough bark and trunks of *Pseudotsuga*
Central Plot
Parmelia Community
Lecanora-Lecidea Community
On smooth bark of trunks of *Pseudotsuga*
Southern Plot
Parmelia Community
Lecanora-Lecidea-Rhizocarpon Community
On twigs and branches of crown of *Pseudotsuga*
All plots
Parmelia-Cetraria Community
Northern Plot
Alectoria-Letharia Community
Central Plot
Alectoria-Letharia-Usnea Community
Southern Plot
Xanthoria Community
Alectoria-Letharia-Evernia-Usnea Community

Abies grandis/Pachistima Association
On soil
Northern Plot
Peltigera Community
Central Plot
Peltigera-Cladonia Community
Southern Plot
Peltigera-Cladonia-Lobaria Community
On rotten wood
All plots
Cladonia Community
On smooth bark of *Amelanchier*
Southern Plot
Lobaria Community
Bacidia-Bilimbia-Pertvssaria-Rinodina Community
On smooth bark of trunks of conifers (mostly *Pseudotsuga*)
Southern Plot
Lecanora-Lecidea Community
Central Plot
Lecanora-Lecidea-Ochrolechia Community
On crown branches of all conifers in plots
All plots
Parmelia-Cetraria Community
Southern Plot
Alectoria Community
Northern and Central Plots
Alectoria-Letharia Community

Bryophyte Communities

Festuca/Symphoricarpos Association
On soil
Northern Plot
Brachythecium-Ceratodon-Eurhynchium-Pohlia-Tortula Community
Central Plot
Brachythecium-Encalypta-Riccia-Tortula Community
Southern Plot
Brachythecium-Bryum-Camptothecium-Ceratodon-Didymodon-Eurhynchium-Funaria-Leptobryum-Pohlia Tortula Community

Symphoricarpos/Festuca Association
On soil
Northern Plot
Brachythecium-Ceratodon-Tortula Community
Central Plot
Brachythecium-Ceratodon-Claopodium Community
Southern Plot
Brachythecium-Bryum-Ceratodon-Tortula Community
On *Crataegus* bark
Central Plot
Homalothecium Community

Pinus ponderosa/Agropyron Association
On soil
Northern Plot
Central Plot
Tortula-Polytrichum Community
Southern Plot
Ceratodon-Ptychomitrium-Rhacomitrium-Rhodobryum Tortula Community
On rocks
Central Plot
Grimmia-Tortula Community
Southern Plot
Camptothecium-Ceratodon-Ptychomitrium-Rhacomitrium-Rhodobryum-Tortula Community

Pinus ponderosa/Symphoricarpos Association
On soil
Northern Plot
Barbula-Brachythecium-Bryum-Eurhynchium-Polytrichum-Rhytidiadelphus-Tortula Community
Central Plot
Brachythecium-Bryum-Eurhynchium-Hypnum-Rhytidiadelphus-Tayloria-Tortula Community
Southern Plot
Aulacomnium-Brachythecium-Bryum-Camptothecium-Cephalozziella-Ceratodon-Dicranum-Drepanocladus-Onchophorus-Orthotrichum-Polytrichum-Rhytidiadelphus-Timmia-Tortula Community
On rocks
Northern Plot
Grimmia-Polytrichum-Timmia Community
On wood
Southern Plot
Aulacomnium-Brachythecium-Camptothecium-Cephalozziella-Grimmia-Ceratodon-Dicranum-Polytrichum-Timmia-Tortula Community
On bark
Southern Plot
Orthotrichum Community

Pseudotsuga/Physocarpus Association
On soil
Northern Plot
Atrichum-Polypodium-Ceratodon-Dicranum-Grimmia-Mnium-Orthotrichum-Polytrichum-Rhytidiadelphus-Timmia-Tortula Community
Central Plot
Brachythecium-Camptothecium-Eurhynchium-Orthotrichum-Tayloria-Pseudisothecium-Rhytidiadelphus-Rhytidiopsis Community
Southern Plot
Aulacomnium-Brachythecium-Camptothecium-Claopodium-Polytrichum-Rhacomitrium-Rhytidiadelphus-Tortula Community
On rocks
Northern Plot
Grimmia Community
Southern Plot
Anacolia-Antitrichia-Brachythecium-Camptothecium-Didymodon-Grimmia-Hedwigia-Homalothecium-Lophozia-Neckera-Mnium-Tortula-Orthotrichum-Polytrichum-Porella-Rhacomitrium Community
On wood
Central Plot
Brachythecium-Dicranum-Eurhynchium-Mnium Community
Southern Plot
Cephaloziella-Dicranum Community
On bark
Central Plot
Brachythecium-Eurhynchium-Orthotrichum Community
Southern Plot
Brachythecium-Claopodium Community

Abies grandis-Pachistima Association
On soil
Northern Plot
Aulacomnium-Brachythecium-Caliergoniella-Dicranum-Orthotrichum-Rhacomitrium-Rhytidiadelphus-Mnium-Timmia Community
Central Plot
Brachythecium-Caliergoniella-Camptothecium-Dicranum-Timmia-Drepanocladus-Eurhynchium Community
Southern Plot
Eurhynchium-Polytrichum-Rhytidiadelphus Community
On wood
Northern Plot
Dicranum Community
Southern Plot
Camptothecium-Dicranoweisia-Dicranum-Orthotrichum-Polytrichum-Ptilidium-Scapania Community
On bark
Northern Plot
Drepanocladus Community
Central Plot
Dicranum Community

ADDITIONAL OBSERVATIONS ON BRYOPHYTES

The collections included 79 species of mosses and liverworts. Table 4A gives their distribution throughout the plots. Some of the species grew on rocks, others on soil, others on duff and litter on the forest floor, others on rough bark at the base of older conifer trees, especially *Pinus ponderosa* and *Pseudotsuga taxifolia* var. *glauca*, and others on the bark of such shrubs or small trees as *Philadelphus, Acer, Salix* and *Amelanchier*. Bryophyte communities are listed in table 11.

DISCUSSION

In eastern Washington and adjacent Idaho precipitation occurs chiefly in the fall, winter, and spring with the summers normally characterized by drought. The trips made to the plots in the summer of 1949 were designed to check the effect of the dry summers on the fungus population and, as expected, little fruiting was found at this time except for a few parasitic fungi. Presumably their spores had germinated and started infection during the more moist late spring after the new leaves of the host plant had started to develop. Throughout the period of study most fungus fruiting was initiated following early fall rains, but many fruited in late spring; as total rainfall increased the fruiting of fleshy fungi increased. If there were dry periods between periods of precipitation, fruiting of fleshy fungi tended to decrease, or at least did not increase. If the rains were continuous throughout the period from the early rains to the end of the season as indicated by snowfall, which does not inhibit fruiting but which prevents collecting, fruiting of fleshy fungi was exceptionally vigorous.

Moisture stick, soil temperature and macroclimatic temperature records, when compared with the number of fungus fruit bodies collected, proved rather inconclusive. However, comparison with precipitation, and some temperature records, has given good correlation over a 3-year period.

Since the study was confined to an area in which the parent material of the soil was loess, glacial, granitic or basaltic, and thus not comparable to the contrasted calcareous or sandy soils of many other workers, there is little basis for comparison between the results of this study and those studies made in Europe. It is well known that a number of ubiquitous species inhabit various types of forest throughout the northern hemisphere, but not enough work of an intensive type has yet been done in North America to indicate the breadth of tolerance of the species herein involved. Uncertain taxonomic position of many of the species makes accurate comparison between species found on these plots and elsewhere in North America unsatisfactory.

The distribution of pathogenic and saprobic fungi in different associations is governed by their host and substratum preferences which, as noted above, may be retricted in some cases or exceedingly broad in others. Host restriction of an obligate parasite restricts the fungus from those associations in which the host is absent. Fungi such as *Hymenochaete tabacina* (Sow. ex Fr.) Lév. are widely distributed throughout the associations in which they occur because they have a wide substratum tolerance and appear to grow on any woody and some herbaceous substrates.

In the plots studied some species appear to be restricted to grass-dominated unions. This restriction may include *Pinus ponderosa/Agropyron* as well as *Festuca/Symphoricarpos* stands. Other soil species are restricted by reason of mycorrhizal relationships with certain host plants, especially Boletaceae and certain species of lamellate fungi.

It appears that in general the lichens of the plots found on tree bark and rotten wood have closer affinities with those of northern and montane habitats; those found on rocks have closer affinities with species found on rocks in cooler dry regions. The taxonomic status of most groups of lichens appears in such a state of flux, either from fine splitting as in the case of Cladonia, Alectoria, Peltigera and Parmelia, or from lack of recent monographic treatments as in the case of many crustose groups on different types of rocks and tree bark, or from lack of agreement between lichenologists concerning specific limits, that further discussion of geographic affinities is premature.

From the literature it is indicated that the forest mosses of this region have greater affinity with species of wide distribution in the northern parts of the continents of the northern hemisphere whose distributions tend to extend southward along the higher mountain ranges such as the Rocky Mountains.

Pacific coastal climatic influences are indicated in this region especially by the Thuja-Tsuga forests which occur immediately above the highest association covered by this study. Thus, of the mosses usually restricted to the area west of the Cascade Mountains, it should not be too surprising to find some extending inland into the northern Rockies which are subjected to mild oceanic influences. According to Koch's (1950) terminology, the following selected species found during this study have the indicated distribution: Cosmopolitan: *Ceratodon purpureus, Polytrichum juniperinum;* Circumboreal: *Rhytidiadelphus triquetrus, Atrichum undulatum;* Bipolar montane: *Didymodon recurvirostris, Tortula ruralis;* Arctic montane: *Brachythecium albicans, Encalypta rhabdocarpa;* Boreal America: *Brachythecium asperrimum;* Pacific Coast: *Ptychomitrium gardneri, Pseudisothecium stoloniferum.*

SUMMARY

1. Eighteen plots, three in each of six vegetation associations, in eastern Washington and adjacent Idaho, were studied to determine possible differences in species composition, relative abundance, substratum preference and seasonal appearance of fruit bodies of larger fungi.

2. During three trips to each plot in three fall and three spring seasons fruit bodies of all species of

fungi found were collected, counted or estimated, and all species found of lichens and bryophytes were collected. Comparative studies of paired plots are needed to determine whether or not picking of fruit bodies has an adverse effect on the mycelium.

3. Within the area there was sufficient uniformity in physical and chemical properties of the soils that differentiation of fungus populations on this basis was not evident.

4. Macroclimatic data were of little use in determining the temperature and the amount of precipitation received by the plots but certain trends in variation of microclimatic factors were obtained by soil temperature and moisture stick determinations. During spring, soil temperature declines progressively through the altitudinal series of associations, but no regular pattern is followed as the soil cools in the fall.

5. Precipitation: temperature ratios of various types indicated no general formula which could be used to predict the rhythm of spring and fall fruiting. Fall fruiting was more easily correlated with precipitation, spring with soil temperature.

6. Burial of pieces of cloth in the soils of the plots, and subsequent testing for evidence of microbiological activity, indicated a greater amount of cellulosic activity in prairie than in forest plots. Whether the same organisms were present but more active under warmer temperatures was not determined.

7. Of the 815 species of fungi collected only 31 appear to be restricted to the xerophytic grassland associations, the remainder were associated with shrub or forest associations.

8. In the area studied, fungi fruit sparingly in summer because of drought, and winter temperatures inhibit activity, so that most fruit bodies appear in spring or fall. At the lowest and most xerophytic extreme of the series of associations nearly as many fungi fruit in spring as in fall, but in progressively higher and more mesophytic associations more and more fungi fruit in the fall than in the spring.

9. If the rainy season starts early in the fall and precipitation is maintained at a constantly high level more fungi fruit and the fruit bodies are on the average larger than if precipitation starts late, or than if precipitation starts early and is interrupted.

10. There is a relatively low degree of constancy in fungi among stands in each of the associations studied. Constancy appears to increase in the more moist associations where the fungus population is richer, but there is evidence that this is largely a result of dryness regularly inhibiting the fruiting of mycelia that are also common in the lower and drier associations.

11. Fidelity analyses indicate for the fungi of each association a greater affinity in the direction of more mesophytic associations, this may simply reflect the increasing richness of the fungus populations, or more regular fruiting, in progressing upward through the series of associations.

12. Dominance, determined by the volume of space occupied by all the fruit bodies of a species observed, was found to have physiognomic rather than competitive significance.

13. Of the 145 species of lichens and 79 species of bryophytes collected in these plots some appear restricted to certain types of habitat, others have a wide ecologic amplitude.

14. From the lowest altitudinal association upward through the zonal sequence, constancy of lichen and bryophyte species increases.

15. The lichen flora of the prairie vegetation (grassland and shrub associations) is distinctly impoverished by comparison with that of the forest associations. Impoverishment at low altitudes is almost as striking in fungi, but is slight in mosses.

16. Ecotones generally seem more inviolate toward the lower end of the zonal sequence, especially for the lichens.

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The following workers have co-operated with the identification of species in the groups of organisms indicated: R. A. Cain, University of Toronto, resupinate Hydnaceae; E. K. Cash, National Fungus Collections, Inoperculate Discomycetes; C. W. Dodge, Missouri Botanical Garden, *Onygena;* M. S. Doty, University of Hawaii, Clavariaceae; C. E. Emmons, National Institutes of Health, *Microsporum* and *Thielavia;* the late H. S. Jackson, University of Toronto, and John Eriksson, University of Uppsala, Sweden, resupinate Thelephoraceae; B. B. Kanouse, University of Michigan, certain Operculate Discomycetes; J. L. Lowe, New York State College of Forestry, resupinate Polyporaceae; G. W. Martin, State University of Iowa, Myxomycetes and some saprobic Hetrobasidiomycetes; J. K. Middleton, University of California Citrus Experiment Station, *Pythium;* J. H. Miller, University of Georgia, Pyrenomycetes; K. B. Raper, University of Wisconsin, *Penicillium* and *Aspergillus;* D. P. Rogers, New York Botanical Garden, certain resupinate Thelephoraceae; F. J. Seaver, New York Botanical Garden (retired), Operculate Discomycetes; C. G. Shaw, The State College of Washington, *Peronospora;* R. Singer, Instituto Tilloa, Tucuman, Argentina, Boletaceae; A. H. Smith, University of Michigan, Agaricaceae; D. E. Stuntz, University of Washington, *Inocybe.* All lichen identifications were made by J. W. Thomson, Jr., University of Wisconsin; certain additional items were determined by A. H. Magnusson, Göteborg, Sweden. All identifications of mosses were made by H. S. Conrad, Grinnell, Iowa. Most of the liverworts

were identified by M. Fulford, University of Cincinnati; those inadvertently mixed with mosses were identified by H. S. Conrad. A complete set of named fungi is filed in the Herbarium of the Department of Plant Pathology, The State College of Washington, Pullman.

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ECOLOGICAL STUDIES OF *BROMUS TECTORUM* AND OTHER ANNUAL BROMEGRASSES

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INTRODUCTION

Bromus tectorum is the most widespread and successful of the annual bromes introduced from Eurasia in many of the semi-arid parts of western United States, particularly in the Columbia Basin and much of the Great Basin. Millions of acres where the native vegetation has been severely disturbed by grazing, fire, or cultivation are now dominated by this grass. It is so aggressive that in many places perennial grasses replace it very slowly through natural processes. Similarly, the success of efforts to reseed perennial grasses on range land dominated by *Bromus tectorum* is often in proportion to the degree of elimination of the Bromus. To enable such reseeding research to proceed efficiently, a knowledge of the root systems, germination requirements and other ecological characteristics of *B. tectorum* was needed, but most research pertained to management of range land on which it occurred (Fleming *et al.* 1942; Hull 1949; Hull & Pechanec 1947; Hull & Stewart 1948; Hurtt 1939; Jackman 1945; Pechanec & Hull 1945; Platt & Jackman 1946; Rummell 1946; Stewart & Hull 1949; and Stewart & Young 1939). Awareness of the need for such fundamental knowledge of *B. tectorum* stimulated the undertaking of this study.

Most of the emphasis was placed on *Bromus tectorum,* but nine other species of annual bromes occurring in or near southeastern Washington were included for comparative information. The species studied are:[2]

[2] The nomenclature of the grasses follows Hitchcock (1950). For plants other than grasses the nomenclature follows Davis (1952).

Section Bromium	Section Eubromus
Bromus brizaeformis	*Bromus rigidus*
B. secalinus	*B. sterilis*
B. commutatus	*B. rubens*
B. mollis	*B. tectorum*
B. racemosus	
B. japonicus	

These species, none of which is native to North America, grow naturally in the Columbia Basin of Washington, Oregon and Idaho. Being winter annuals, they typically germinate when sufficient fall rains occur, develop to maturity and die in the early part of the next summer.

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[1] This research was carried on mostly at the Department of Botany, State College of Washington, Pullman.

The State College of Washington; J. L. Schwendiman, Soil Conservation Service; D. B. Lawrence, University of Minnesota. Mrs. Anne E. Hatley, Pullman, Washington and Harry Wall, Lewiston, Idaho each gave permission to use portions of their land for experimental areas.

AREAS STUDIED

Over 400 experimental plantings were made at the Lewiston (Idaho) Study Area and even more at the Pullman (Washington) Study Area, in addition to laboratory and greenhouse studies and many field observations of the annual bromegrasses occurring in Washington, Oregon, Idaho and Montana.

At both study areas row plantings were made of 10 species of annual bromes to obtain comparative information. In addition, row plantings of 22 collections of *Bromus tectorum* from different geographic places were made to study the genetic variation within this species. For studying the effect of plant density on shoot and seed production, for studying root systems and soil moisture, for clipping studies, and for fertilizer studies, a series of square meter plots were broadcast planted at four densities with *Bromus tectorum* seed[3] collected locally.

LEWISTON STUDY AREA

The Lewiston Study Area was located on the south-facing side of the Clearwater River Valley about 4 mi north of Lewiston, Nez Perce County, Idaho. The elevation of the study area was 350 m (1150 ft), which is 120 m (400 ft) above the valley bottom and about 600 m (2000 ft) below the elevation of the plateau-like Palouse country into which the river has cut its steep-sided valley.

Because of their steepness many of the valley slopes have not been cultivated. On such areas grazing has been heavy, which is thought to be an important factor responsible for the abundance of *Bromus tectorum*. The climate and soils are well suited to *B. tectorum*, and once established, it is not easily replaced by native grasses through natural succession. The more gentle slopes near the study area have been used for wheat production by the summer fallow (alternate year cropping) method. The study area itself (about 800 sq m or 0.2 A) once was on the edge of such a wheat field, but was isolated some years ago by relocation of the highway. Since that time the area had not been grazed or otherwise disturbed, and supported a nearly pure stand of *B. tectorum* when experimentation was started. About 10 plants of *Agropyron spicatum*, and occasional plants of the following were present: *Lupinus leucophyllus*, *Sisymbrium altissimum*, *Sitanion hystrix*, and *Poa secunda*. Around the edges of the study area *Chrysothamnus nauseosus* was frequent, but it was absent where the plots were located.

This site was well suited to a study of *Bromus tectorum* because (1) it is located in a region where *Bromus tectorum* perpetuates itself vigorously on misused range land or land abandoned after cultivation, (2) the soil is a loam which facilitated cultural operations and root and soil moisture studies at all seasons, (3) the soil and slope are remarkably uniform and (4) the area was readily accessible and yet free of disturbance from livestock or man.

The soil was a loam belonging to the Chestnut Great Soil Group. The texture was rather uniform (Table 1). Rocks were absent and pebbles exceedingly rare, so a King tube worked well for obtaining samples for moisture determination. From a depth of about 1.5 to at least 3 m the soil material was cemented into a caliche layer.

TABLE 1. Mechanical analysis by the hydrometer method of the soil at the Lewiston Study Area.

Depth dm	Sand (>0.05 mm)	Coarse silt (0.05-0.005 mm)	File silt (0.005-0.002 mm)	Clay (<0.002 mm)
	%	%	%	%
0-2	39	41	5	15
2-4	41	40	5	14
4-6	38	45	5	12
6-8	40	43	5	12
8-12	45	40	6	8
12-16	45	42	4	9

The mildness of the winters (Table 2) was indicated by the increase in the number of tillers and growth in length of the leaves of Bromus plants during the months of December, January, and February, 1950-51. Snow covered the area only occasionally. The soil was wetted at least down to the caliche layer during the winter, but precipitation during the summer was insufficient to replace moisture removed from the soil by evaporation and plant use.

TABLE 2. Climatological data from the Lewiston Water Plant 4 mi. south of the Lewiston Study Area and precipitation at the Study Area.

Month	Lewiston Water Plant (elev. 226 m)						Ppt at Study Area (elev. 350 m), in.
	Highest temp °F	Lowest temp °F	Mean temp °F	Normal ppt in.	Actual ppt in.	Depth of snow, sleet & hail, in.	
1950							
September	104	32	65.3	.90	.46	0	.50
October	83	28	55.2	1.23	2.87	0	3.04
November	75	26	44.3	1.50	1.88	0	1.97
December	55	28	42.4	1.47	2.19	0	2.72
1951							
January	55	4	35.4	1.41	.94	0.2	.93
February	55	12	38.9	1.22	.62	0.6*	.78
March	68	22	42.3	1.22	.78	T	1.87
April	80	23	53.2	1.12	.33	0	.35
May	94	33	60.7	1.49	.83	0	.92
June	95	35	65.1	1.46	2.01	0	.79
July	106	48	75.6	.48	.23	0	.27
August	102	45	72.6	.48	.39	0	.55
Total	—	—	—	13.98	13.53	0.8	14.69
Average	—	—	54.2	—	—	—	—

*Record missing for Lewiston Water Plant. Value given is for Lewiston Weather Bureau, 2 mi. further south at the airport.

[3] Seed is often used throughout the paper to stand for floret. The palea and lemma are adherent to the mature fruit, so all planting and germination studies were conducted using complete florets.

Part of the experimental area was spaded in April and May, 1950, and kept free of plants during the summer to reduce the number of Bromus seeds that would be present to contaminate the plantings. Spading was successful in this respect, but it also resulted in a greater soil moisture content at the end of the summer than in unspaded areas and probably resulted in an increase in nutrient supply through decay of organic matter. However, the artificially planted plots used for testing the effect of fertilization were not spaded until October, 1950, so that nutrient and moisture supply were unaffected by fallowing the soil.

Because the soil did not remain sticky after a rain, it was possible to plant and cultivate at the desired times. This facilitated control of weeds and volunteer Bromus, so that in the row plots a highly satisfactory stand was obtained essentially free of contamination.

Pullman Study Area

The Pullman Study Area was located just south of the Forestry Nursery near the campus of the State College of Washington at Pullman, Whitman County, Washington. The elevation was 790 m (2600 ft) above mean sea level. The area sloped very gently to the south. Previously a pasture, it had been unused for several years, and supported a stand of grasses and forbs. About 900 sq m (0.25 A) were plowed, disked and harrowed in the summer of 1950.

The Pullman Study Area proved to be distinctly less useful than the Lewiston Study Area, thus few data were collected in it. Factors which reduced its value below that which was anticipated were (1) very troublesome weeds, (2) the soil, a silty clay loam, became unworkable when wet, (3) the fall of 1950 was wet for long periods, so that planting and cultivation could not be carried on at the desired times.

Table 3. Climatological data from the Pullman Experiment Station 1 mi. north of the Pullman Study Area and precipation at the Study Area.

Month	Pullman Experiment Station (elev. 777 m)						Ppt at Study Area (elev. 760 m), in.
	Highest temp °F	Lowest temp °F	Mean temp °F	Normal ppt in.	Actual ppt in.	Depth of snow, sleet & hail, in.	
1950							
September	98	27	61.4	1.15	.70	0	.31
October	75	28	49.8	1.59	3.45	0	3.92
November	64	16	39.0	2.76	2.33	–	2.77
December	54	15	38.3	2.69	2.23	9.5	2.81
1951							
January	48	– 5	29.4	2.68	1.51	13.8	–
February	53	4	34.2	2.08	1.33	3.3	–
March	61	18	35.4	2.17	1.09	13.3	–
April	75	21	48.6	1.48	.43	T	.53
May	88	30	53.9	1.48	.69	0	.73
June	80	33	59.1	1.30	1.65	0	1.82
July	96	46	69.0	.49	.30	0	.38
August	92	43	66.8	.53	.88	0	.94
Total	–	–	–	20.40	16.59	39.9	–
Average	–	–	48.7	–	–	–	–

As a result the row plantings were contaminated by local *Bromus tectorum*.

The climate at the Pullman Study Area was distinctly cooler and wetter than at the Lewiston Study Area (Table 3). Because of the more favorable water relations for plant growth, *Bromus tectorum* does not persist as a dominant for many years on land abandoned from cultivation as it does at Lewiston. However, it is abundant on recently disturbed soil, and persists in small amounts indefinitely.

Field Observations

Numerous trips, totaling 5700 mi, were made in eastern Washington, northeastern Oregon, northern Idaho, and western Montana specifically to study and collect the annual bromegrasses in the field. These observations and collections proved useful in providing information on distribution, commonness, and habitats of the various grasses, and helped in understanding the applicability of results in the experimental plantings to natural conditions.

TAXONOMY

The 10 species of *Bromus* considered in this study belong to two sections of the genus. Four species belong to the section Eubromus in which the florets have sharp calluses and barbed lemmas and awns. The 6 species in the section Bromium have less pointed calluses, barbless lemmas and awns, and broader, less compressed glumes and lemmas than those in the section Eubromus.

Relationships of the Species

Of the 6 species in the section Bromium, *Bromus brizaeformis* and *B. japonicus* seem to be distinct entities, even though it sometimes is difficult to distinguish immature or depauperate specimens of *B. japonicus* and *B. commutatus*. The other 4 species, *B. secalinus*, *B. commutatus*, *B. mollis*, and *B. racemosus*, are much alike and may possibly all belong to one species. At least *B. secalinus* and *B. commutatus* appear to belong in one species and *B. mollis* and *B. racemosus* in another.

Distinction between *B. secalinus* and *B. commutatus* is made chiefly on the basis of pubescence on the leaf sheath, *B. secalinus* being nearly or entirely glabrous. Only two collections of *B. secalinus* were made by the writer, one in Umatilla County, Oregon and the other in Lewis County, Idaho. The Oregon collection is doubtful as to identity, as the sheaths have sparse hairs. The Idaho collection, which is typical of the species as described by Hitchcock (1950), was found in a clover hay field. The source of the clover seed was not ascertained, but it may have recently been brought in from another part of the country.

Specimens of *B. secalinus* in the herbarium at the State College of Washington had been collected in southeastern Washington and adjacent Idaho from 1891 to 1911. Visits were made in 1950-52 to several of the specific locations where these collections had been made as well as to numerous other places in that region. Every specimen found had distinctly pubes-

cent leaf sheaths and was considered to be *B. commutatus*. Apparently *B. secalinus* has declined and *B. commutatus* has increased in this area in the last 40 years. Perhaps this is due to a greater competitive ability on the part of *B. commutatus* than of *B. secalinus*. Another possibility is that the two species can cross and that gene flow has occurred causing the change in pubescence in the population previously called *B. secalinus*.

Similarly, *B. racemosus* is distinguished in North American material from *B. mollis* by a lack of pubescence on the lemmas and glumes, lemmas of the latter species being pubescent. *B. mollis* was a much commoner species in the Columbia Basin, occurring in all locations where *B. racemosus* was found. Gradations in degree of pubescence were observed. These facts make it seem plausible that these groups can interbreed. This possibility is supported by the work of Knowles (1944) in California, in which it was found that *B. racemosus* was completely compatible with *B. mollis*. Hybrid seeds were readily produced, the F_1 hybrid was vigorous, its cytological behavior resembled both parents, and the hybrid was completely fertile.

In the section Eubromus the four species studied appear distinct from each other.

Counts of chromosome numbers (Table 4) indicate that two species are diploid and four usually tetraploid in the section Bromium. In the section Eubromus two are diploid, one a tetraploid, and one commonly an octoploid. (Cytogenetic studies on these and other grasses are summarized by Myers, 1947). These chromosome numbers give some support and no disagreement with the possible relationships stated above. For example, the four groups in the section Bromium that were thought possibly to belong to one species (*B. secalinus*, *B. commutatus*, *B. mollis*, and *B. racemosus*) are all commonly tetraploids.

TABLE 4. Chromosome numbers of the ten species of *Bromus* considered in this study.

Species	2N number	Authority
Section Bromium		
Bromus brizaeformis	14	Avdulov (1931)
B. secalinus	14	Nielson (1939)
	28	Avdulov (1931); Cugnac & Simonet (1941); Knowles (1944); Nakajima (1931); Stählin 1929)
B. commutatus	28	Knowles (1944)
	56	Nielsen & Humphrey (1937); Nielsen (1939)
B. mollis	28	Avdulov (1931); Knowles (1943); Knowles (1944); Stählin (1929); Stebbins & Love (1941)
B. racemosus	28	Knowles (1944); Maude (1940)
B. japonicus	14	Avdulov (1931); Stählin (1929); Nielsen & Humphrey (1937)
Section Eubromus		
Bromus rigidus	42	Cugnac & Simonet (1941)
	56	Avdulov (1931); Knowles (1944); Stählin (1929); Stebbins & Love (1941)
	56, 70	Beck & Horton (1932)
B. sterilis	14	Cugnac & Simonet (1941); Stählin (1929)
B. rubens	28	Beck & Horton (1932); Knowles (1944); Stählin (1929)
B. tectorum	14	Avdulov (1931); Cugnac & Simonet (1941); Knowles (1944); Stählin (1929)

A factor contributing to the taxonomic confusion of these annual bromegrasses may be that self-pollination is the rule. Troll (1931) demonstrated self-pollination in *Bromus mollis*, and considered that it and many other bromegrasses were cleistogamous. Beddows (1931) found no cleistogamy in *B. tectorum*, *B. sterilis*, or *B. hordaceous* (*mollis*). He reported a greater variation in progeny resulting from seed from open grown plants than from seed produced in bagged inflorescences, and so considered that cross pollination occasionally occurred. Knowles (1943) considered *B. mollis*, although not cleistogamous, to be highly self-pollinated. He found a high degree of uniformity within each row sown from a single panicle. Others (Smith 1944, Knuth 1908) concurred in the belief that these annual bromes are highly self-fertile and that self-pollination is the rule. The filaments are short and it is believed that the stigmas are generally pollinated by direct contact with the anthers. The writer never observed anthers of any of the annual bromegrasses to be exserted.

Other personal observations support the idea that self-pollination is the rule. *Bromus tectorum* often has pubescent lemmas, but occasionally nearly glabrous (scaberulent) lemmas occur. Collections of florets of these two types were made from plants growing intermixed, therefore distance did not prevent crossing. The progeny of the collections of these two types were nearly all like the parent.

Evidence of the highly self-fertile nature of both *B. tectorum* and *B. rubens* was obtained in the greenhouse. Plants of these two species flowered in the winter (at different times) and each produced an abundance of viable seed.

Inflorescences of *B. tectorum* plants growing in the field near Pullman, Washington, were bagged prior to anthesis in the spring of 1950. All six bagged inflorescences produced a normal amount of seed, which was later tested and found completely viable.

Since self-pollination leads to homozygosity, minor morphological variations can be perpetuated and make the delineation of taxonomic units difficult. This may account in part for the recognition of species of doubtful validity.

Since the annual bromes studied are native to Eurasia, floras from Europe and the Mediterranean areas were consulted to see if they would clarify the taxonomic units of the annual bromegrasses. The confusion of species and synonomy indicated that little help could be obtained from such sources. It appears that nothing less than a monographic study of the group from a worldwide viewpoint will clarify the situation.

For these reasons the treatment by Hitchcock (1950) has been followed in this study even though it is likely that changes are needed to conform to modern species concepts. Hitchcock indicated the need for changes by saying:

"The species of the group containing *Bromus*

TABLE 5. Sources of seeds of *Bromus tectorum* used for studying variability

Country	State	County	Place	Collector
Canada	B. C.		Kamloops	A. McLean, Dominion Range Exp. Sta.
Israel			Jerusalem	Hugo Boyko, Ministry of Agriculture
United States	Calif.	Nevada	Near Truckee	H. M. Laude, Univ. of Calif., Davis
"	Calif.	Tehama	Near Bowman	L. K. Mann, Univ. of Calif., Berkeley
"	Conn.	Tolland	Storrs	G. S. Torrey, Univ. of Conn., Storrs
"	Conn.	Litchfield	Gaylordsville	F. E. Egler, Aton Forest, Norfolk
"	Idaho	Butte	SE of Arco	D. L. Goodwin, State College of Wash., Pullman
"	Idaho	NezPerce	Near Lewiston	Writer
"	Kan.	Ellis	Hays	H. H. Hopkins, Kansas State College, Hays
"	Mich.	Ingham	Near East Lansing	W. B. Drew, Mich. State College, East Lansing
"	Mont.	Ravalli	Near Florence	R. A. Peterson, U. S. Forest Service, Missoula
"	Mont.	Glacier	Near Babb	D. M. Lynch, State College of Wash., Pullman
"	Nev.	Humboldt	Winnemucca	H. M. Laude
"	Nev.	Washoe	Reno	W. D. Billings, Duke Univ., Durham, N. Car.
"	N. Dak.	Stark	S. of Belfield	L. D. Potter, N. Dak. Agr. College, Fargo
"	Ore.	Morrow	E. of Boardman	Writer
"	Ore.	Umatilla	W. of Pendleton	Writer
"	Ore.	Wallowa	NW of Enterprise	Writer
"	Ore.	Wheeler	SE of Fossil	Writer
"	Wash.	Okanogan	Nespelem	Mrs. X. M. Gaines, State College of Wash., Pullman
"	Wash.	Skagit	Deception Pass	H. M. Austenson, State College of Wash., Pullman
"	Wash.	Whitman	Near Pullman	Writer

secalinus, B. commutatus, B. mollis, and *B. racemosus* are closely allied, differentiated only by arbitrary characters. The forms are recognized as species in most recent European floras and this disposition is here followed."

This discussion is given to point out the need for care in applying the results described in this paper to populations of these species not included in this study.

Herbarium specimens of the bromegrasses studied by the writer have been deposited in the herbarium of the State College of Washington.

VARIABILITY IN *Bromus tectorum*

Knowledge obtained through study of one population can be applied wisely to another population of the same species only if the change in response caused by genetic differences can be evaluated. To obtain indications of the genetic variation in *Bromus tectorum*, collections from various localities (Table 5) were planted at the Lewiston and Pullman Study Areas.

Each seed lot, collected at maturity in 1950, was planted in the early fall (Oct. 1, 1950), late fall (Nov. 11) and spring (Apr. 2, 1951). Three rows about 1 m long and 25 cm apart were sown at each date. The fall plantings germinated promptly, but due to lack of moisture the spring plantings did not germinate until after April 28. Herbarium specimens were collected 12 times from each fall sowing of each collection. These specimens, supplemented by written records, furnished a developmental series for later study.

VARIATION IN WINTER HARDINESS

Plants from all the North American collections of *Bromus tectorum* survived the winter in excellent condition; even the tips of the leaves remained green. Appreciable growth occurred in December, January, and February at the Lewiston Study Area, but not at the Pullman Study Area. On the plants of the Jerusalem, Israel collection the leaves died, so that at the end of winter all the plants looked dead. The crowns survived on a few plants of the early fall planting at the Lewiston Study Area, however, and subsequently developed to maturity.

VARIATION IN PHENOLOGY

Plants grown from seed obtained at different geographic locations differed strikingly as to the time: (1) inflorescences emerged, (2) purple coloration de-

FIG. 1. Differences in growth of *Bromus tectorum* planted Oct. 1, left, and Nov. 11, right, in relation to source of seed. Three horizontal rows were planted to each seed source in the following order from front to rear: Kansas, Nevada, British Columbia, Montana, Washington, and Israel (winterkilled). Vertical scale in decimeters. Lewiston Study Area, April 21, 1951.

veloped, and (3) the plants became dry and brown. At the Lewiston Study Area these differences (Fig. 1 & 2) amounted to an extreme of about 25 days in the time of emergence of the inflorescences and to about 20 days in the time when plants became completely brown. Among the North American collections these differences were 19 and 20 days, respectively. These differences are enough to indicate that early and late strains could be selected.

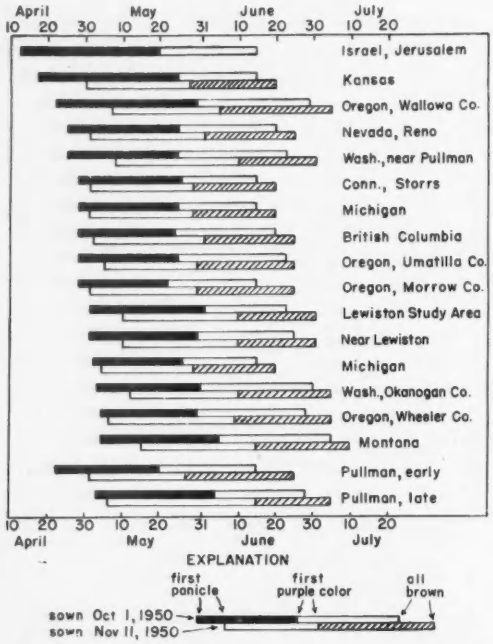

FIG. 2. Phenology of *Bromus tectorum* at the Lewiston Study Area in relation to source of seed. Two lowest collections from two phenological types occurring intermixed at Pullman, Washington.

The variations in time of maturity have little apparent relation to the climate of the locality in which seeds were collected except for those from Jerusalem. These plants were the earliest to mature in spite of the severe winter injury to the few individuals that survived. It seems likely that the very early development of these plants may be of survival value in the eastern Mediterranean climate.

Striking variations in phenology caused by environmental differences were frequently observed. For example, the development of *B. tectorum* was about 14 days earlier in 1950 at the Lewiston than at the Pullman Study Area, the latter being cooler as discussed earlier. Also, on south-facing slopes on the north side of the valley at Lewiston, *B. tectorum* developed purple coloration 21 days earlier at 245 m (800 ft) than at 565 m (1850 ft).

VARIATION IN MORPHOLOGY

Height measurements of the row plantings of *Bromus tectorum* at the Lewiston Study Area are given in Table 6. Because it is difficult to judge the typical or the average of the taller plants in a plot, these measurements may be somewhat in error, but the general indications they show are considered valid. The variation within plantings was small in relation to the variation between plantings. It appears likely that these variations are of genetic origin, indicating that strains of different sizes were present.

TABLE 6. Height measurements of *Bromus tectorum* in the row plots at the Lewiston Study Area, 1951. Plants considered typical of the taller plants in the plot were measured to the nearest 5 mm on Feb. 24 and to the nearest 50 mm on June 2.

Source of seed	Early Fall Planting (Oct. 1)		Late Fall Planting (Nov. 11)	
	Ht, Feb. 24 mm	Ht, June 2 mm	Ht, Feb. 24 mm	Ht, June 2 mm
Connecticut, Storrs	40	600	10-25	400
Michigan (2 coll)	40-50	550-600	20	450
Michigan (1 coll)	45	650	15-20	450
Kansas	45-50	500	20	400
Nevada, Reno	45	600	20	450
British Columbia	40	550-600	20	450
Montana	40	500	20-25	400
Wash., Okanogan Co.	40	550	20	450
Israel, Jerusalem	50 (dead)	200-250	20 (dead)	–
Oregon, Wheeler Co.	40	550	20	450
Oregon, Wallowa Co.	40	550	20	400
Oregon, Morrow Co.	40	550-600	20	450
Oregon, Umatilla Co.	40	550-600	20	450
Wash., near Pullman	40	550-600	20	450
Wash., Pullman	45	550-600	20	450
Idaho, near Lewiston	45	500-550	20-25	400
Lewiston Study Area	45	500-550	25	400
Pullman, late strain	40	550	20	450
Pullman, early strain	45	500	25	350

The small size of the strain from Jerusalem is attributable in large measure to the shorter culms and more contracted panicles.

Variation in pubescence on the spikelets occurs in *Bromus tectorum* as evidenced by the variety *glabratus* which Spenner designated to distinguish those plants with glabrous spikelets from the typical species with pubescent spikelets (Hitchcock 1950). Among the *B. tectorum* grown from seed collected throughout North America, much variation was found in the pubescence on the lemmas. The length of the hairs ranged from tiny protuberances (scaberulent) through short, medium, long to very long hairs, and the density of the hairs ranged from sparse to very thick. Pubescent lemmas were found associated with both ciliate and non-ciliate paleas, but scaberulent lemmas were associated only with non-ciliate paleas. At the time of emergence of the inflorescence, the lemmas on some plants were glabrous but soon became pubescent. In other cases they were pubescent before emergence, although the length of the hairs continued to increase until about the time of anthesis.

The length and density of the pubescence on the lemmas and paleas in 119 collections of *B. tectorum*

from Washington, Oregon, Idaho, and Montana showed the same variation as the plants in the row plantings referred to above. Of the 119 collections, 68% had pubescent spikelets, 19% had scaberulent spikelets, and 13% had both types. Some of those counted as pubescent had hairs so short they bordered on scaberulent.

No other morphological character was noticed as varying in North American material of *Bromus tectorum*. In addition to the difference in winter hardiness and in phenology already mentioned, two morphologic differences from North American plants were noticed in those from Israel. First, the panicles were a little less open than in the North American plants, although not as compact as in *B. madritensis*, the most similar species. Secondly, the florets were broader and flatter. When first examining the florets of this collection, it was thought the seeds were empty, but germination was surprisingly satisfactory. Florets produced on the plants grown at the Lewiston Study Area had this same flat characteristic, so it apparently was not caused by stunting the parent.

In most ways the North American material of *B. tectorum* and this collection from Jerusalem are alike, yet the differences are such as to make the Jerusalem strain distinct from any of the North American strains the writer has studied.

OCCURRENCE, HABITATS AND ECOLOGICAL ROLE

Occurrence and Habitats of Each Species

In common with other annuals, the annual bromes are most frequent on areas of recent disturbance, such as roadsides or fields recently grazed or cultivated. Relationships of *B. tectorum* to grazing in southeastern Washington are discussed by Daubenmire (1940). In some places annual bromes, particularly *B. tectorum* and *B. japonicus*, occurred in stands of vegetation which apparently had not been disturbed much, as has been reported by Daubenmire (1942). Where pure stands of *B. tectorum* have developed following abandonment from cultivation or severe grazing, reestablishment of the native species is very slow, the Bromus persisting for many years as a dominant. Vegetation zones or associations given below are used as described by Daubenmire (1942 & 1952).

SECTION BROMIUM

Bromus brizaeformis and *B. japonicus* were absent from the drier grassland areas examined. In the wetter portions of the *Agropyron/Poa* Association, in the *Agropyron/Festuca* Association and in the *Pinus ponderosa* and *Pseudotsuga taxifolia* forest zones they occurred frequently on roadsides and other disturbed places, and occasionally were found in grazed areas and particularly in rocky soil areas. *B. japonicus* was more common than *B. brizaeformis*, especially in Montana.

Bromus secalinus was found only twice, once in Oregon and once in a clover hay field in Idaho. Apparently it is becoming scarcer and *B. commutatus* is more abundant than formerly, as was suggested in the section on taxonomy.

Bromus commutatus, like the previous 3 species, was absent from the drier grassland areas. It was usually confined to cultivated ground or roadsides, but in the foothills of the Blue Mountains east of Pendleton, Oregon, it was abundant in the grazed ranges in and near the lower edge of the ponderosa pine forest.

Bromus mollis cannot come into as dry areas as does *B. tectorum*, but is able to grow in drier places than *B. commutatus*. Although frequently seen, it was often sparse, generally being a minor constituent of the vegetation. In the Columbia Basin this species and *B. japonicus* were sometimes present in rocky, shallow soil but absent on adjacent deep rock-free soils. This may result because, in dry climates, a greater proportion of rainfall is available for plant use in rocky than in fine-textured soils because of the lesser evaporation loss in the rocky soils (Shaw 1952).

Bromus racemosus was found in the same sites as *B. mollis* but less frequently, being uncommon in the areas studied.

SECTION EUBROMUS

Bromus rigidus was found only in areas of low elevation in Washington, west central Idaho and Oregon, apparently being limited to the warmer areas by susceptibility to winterkilling. It was usually confined to roadsides where it was often abundant.

Bromus sterilis was found only at Pullman, Washington, in the Clearwater River Valley 10 mi above Lewiston, in the Snake River Valley 8 mi below Lewiston, Idaho, and in the foothills 10 mi east of Pendleton, Oregon. It is as winter hardy as, and otherwise similar to, *B. tectorum*, and occurred in Washington as early as 1896 according to herbarium specimens at the State College of Washington. Therefore it is not obvious why this species is so uncommon. Perhaps it is due to a greater susceptibility to damage by smut, *Ustilago bullata*. This possibility is supported by the high frequency of smut often noted in the plantings and natural stands of the grass.

Bromus rubens was listed by Peck (1941) as a characteristic species in the "Bunch-Grass Section" of northeastern Oregon. Three trips were made in 1950 and 1951 into northeastern Oregon to find this species. It was found only in one small area in the lower John Day River Valley about 40 km (25 mi) up from the Columbia River. In 1951 it seemed less abundant than when first seen at this place in 1950, being more restricted the second year to presumably warm sites such as south-west facing slopes. Since all but one plant of this species winterkilled at the Lewiston Study Area in 1950-51 (using seed from the Oregon collection), it seems likely that it is restricted in its range by winterkilling. Perhaps it had become more widespread in northeastern Oregon during a series of favorable winters, only to be nearly all killed during subsequent severe winters.

Bromus tectorum was found at every place visited in the grassland areas of eastern Washington, north-

TABLE 7. Amount of annual species of *Bromus* in little disturbed native grasslands, based on 10 or 11 2 x 5 dm plots per stand. Stands listed approximately in order of increasing wetness of the climate.

Species	Year	No. of plants/ sq dm	Shoot wt, mg/ sq dm*	No. of seeds/ sq dm	Avg. ht, cm	No. smutted, %	Location of stand
				Artemisia/Agropyron Association			
B. tectorum.....	1950	3.4	177	3.7	20	11	Wash., Whitman Co., cemetery SE of Lamont
	1951	1.5	32	0.06	17	8	
				Agropyron/Poa Association			
B. tectorum.....	1951	1.1	18	0.8	15	50	Wash., Adams Co., Palouse Falls
B. tectorum.....	1950	0	—	—	—	—	Wash., Adams Co., N of Washtucna; steep NW slope
	1950	0.05	0.8	0.2	11	0	Same location, but on nearly level top of hill
B. tectorum.....	1950	0.02	3.1	0.05	18	50	Wash., Whitman Co., W of Colton; virgin grassland
	1951	0	—	—	—	—	
B. japonicus.....	1950	5.8	166	18	16	0	Ditto
	1951	4.1	113	11	15	Tr.	
B. brizaeformis...	1950	0	—	—	—	—	Ditto
	1951	0.01	4.5	0.03	20	0	
B. tectorum.....	1950	1.6	10	1.7	24	5	Same grassland but on slightly disturbed portion
	1951	0.1	0.2	0.5	15	0	
B. japonicus.....	1950	2.6	175	12	20	0	Ditto
	1951	2.5	89	6	17	0	
B. brizaeformis...	1950	8.5	56	6.2	21	1	Ditto
	1951	5.2	15	2.3	17	0	
				Similar to the *Agropyron/Poa* Association of SE Washington			
B. tectorum.....	1951	0.2	1.6	0.4	9	8	Mont., Missoula Co., west face of Mt. Sentinel
				Festuca/Agropyron Association			
B. tectorum.....	1951	0.04	0.3	—	—	0	Wash., Whitman Co., State College of Washington Prairie Strip
B. japonicus.....	1951	6.3	154	16	14	3	Ditto
B. tectorum.....	1950	1.0	15	—	—	8	Wash., Whitman Co., Whelan Cemetery NE of Pullman
	1951	0.09	0.6	0.2	19	0	
B. japonicus.....	1950	8.3	172	2.1	29	0	Ditto
	1951	0.8	30	0.4	29	0	
B. brizaeformis...	1950	3.8	172	2.9	24	0	Ditto
	1951	3.0	62	1.6	15	0	

*Air-dry weight of shoot systems.

eastern Oregon, northern Idaho, and western Montana. It usually was common, and often dominant. In the ponderosa pine zone it was frequent to common, and occurred in the stands away from fields and roads. In the douglas fir zone it was mostly restricted to roadsides, trails, or other much disturbed sites. It was confined to sunny, relatively dry roadsides in the arborvitae-hemlock association. A few rare specimens were found along roadsides in the lower spruce-fir zone, but it was not seen in the higher parts of this zone.

QUANTITATIVE STUDIES IN NATIVE GRASSLANDS

In the area of study only a few small stands of 1 to 10 A were known which had not been disturbed considerably by grazing or cultivation. In these stands all the annual bromegrass plants were collected from 10 to 11 2 x 5 dm plots spaced at 2.5 m intervals along a line through each of the stands.

The data (Table 7) indicate that *Bromus tectorum* can persist in competition with little-disturbed native vegetation in small stands. The Bromus plants were spindling and stunted, producing few seeds per plant. *B. tectorum* was the only annual Bromus in the dryer grasslands, but as the soil moisture supply increased *B. japonicus* appeared and became more abundant than *B. tectorum*. *B. brizaeformis* occurred with *B. japonicus* but was less abundant.

There is doubt as to the applicability of these data to large stands. The small seed output per plant in a few of these areas indicates the possibility that the plants growing in these stands may not produce enough seed to maintain the population. The dissemination from the disturbed areas around the edges may be necessary to supplement the seed production in the area. However, rodent excavations may be another source of maintenance of the population and one which would apply to large as well as small areas. In one lightly disturbed stand of the *Agropyron/Poa* Association the number of plants on rodent excavations was twice as great, the shoot weight four times as great, and the seed output nine times as great per unit area as in the rest of the stand.

In the Columbia Basin there are occasional areas where the bedrock basalt, partially cracked and broken, is at the surface except where ridges or patches of soil up to a meter or more deep are scattered throughout the rocky area. On the ridges na-

TABLE 8. Production of *Bromus tectorum* and *B. japonicus* on shallow and adjacent deep soil, based on fifteen 2 x 5 dm plots in the shallow soil and six 1 x 2 dm plots in the deep soil.

Species	Soil depth	Year	No. of plants/ sq dm	Air-dry shoot wt, mg/ sq dm	No. of seeds/ sq dm	Avg. height, cm	No. smutted, %	Location
B. tectorum	shallow	1950	11	177	24	8	8	Wash., Adams Co., 6 mi N of Washtucna
	deep	1950	60	1900	64	20	19	Ditto
B. tectorum	shallow	1951	1.1	64	—	16	53	500 ft. E of Lewiston Study Area
	deep	1951	31	1045	—	14	60	Ditto
B. japonicus	shallow	1951	7.9	270	5.2	12	7	Ditto
	deep	1951	0.08	2	0.3	15	0	Ditto

tive grasses were often sparse or absent and *B. tectorum* formed a dense stand. In the rocky areas *B. tectorum* was sparse, as shown in Fig. 3 and Table 8, being able to grow only in the soil of crevices and cavities among the rocks.

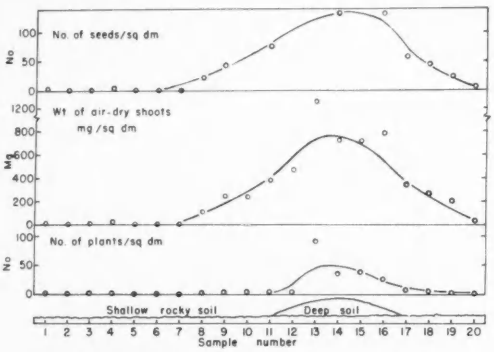

FIG. 3. Density and production of *Bromus tectorum* in 2 x 5 dm plots, 1.8 m apart along a transect across a ridge of deep soil in an area of exposed basalt rock near Lewiston, Idaho, June 15, 1951.

In the transect across a ridge of deep soil (Fig. 3), the number of plants per sq dm fell off sharply at the edge of the deep soil, but the yield of shoots and seeds was fairly high in a rocky strip about 6 m wide on each side of the deep soil. Perhaps the cause is as follows. By dispersal from the plants on the ridge, the adjacent rocky area would have received a much greater number of seeds than areas further away from the ridge. This large seed supply would assure that all available crevices or cavities were occupied by a plant. Further away from the ridge, however, seed supply would be smaller and only part of the available sites would be occupied by plants. A less likely hypothesis is that the depth and number of crevices or some other rock character differed away from the ridge than next to it, thus resulting in the observed differences.

In some shallow soil sites *B. japonicus* and *B. mollis* were more abundant than *B. tectorum*, a reversal from the ratios on the deep soil. One such case is given in Table 8 for an area east of the Lewiston Study Area. Time was not available to study the cause of these intriguing correlations. Ability of the plants to rapidly establish root systems in the crevices seems to be a likely cause. The greater root development (discussed later) of *B. japonicus* than of *B. tectorum* might account for the relatively greater success of *B. japonicus*, but this would not explain the success of *B. mollis*, as it is believed to have a smaller root system than *B. tectorum*. Perhaps another factor, or more likely a combination of factors, provides the explanation.

GROWTH AND REPRODUCTION

WINTER HARDINESS AND PHENOLOGY OF THE SPECIES

Of the 10 species tested, all survived the winter of 1950-51 in good condition at the Pullman and Lewiston Study Areas except *B. rubens* and *B. rigidus* which winterkilled completely at the Pullman Study Area. One plant of *B. rubens* and about one-fourth of the *B. rigidus* plants survived at the Lewiston Study Area.

In October 1953 the following species were planted in Minneapolis, Minnesota, in short-row plots A minimum thermometer lying on the ground surface in the plots recorded a minimum temperature of −10°F (−23°C) during the winter. In the spring the following results were observed:

B. tectorum (N. Am. collections). Very slight injury to leaves
B. japonicus and *B. sterilis*..... Slight injury to leaves
B. commutatus..... Considerable injury to leaves
B. brizaeformis..... Few apparently killed, all injured somewhat
B. racemosus and *B. mollis*..... Much injury; about one-half of plants killed
B. rigidus and *B. rubens*..... All killed

In the row plots at the Lewiston Study Area in 1951 the first species to produce inflorescences was *B. sterilis* (April 22), the latest *B. secalinus* (May 20). The time of maturity and death varied from June 18 (*B. sterilis*) to July 8 (*B. japonicus*), a difference of three weeks. *B. secalinus* and two other species produced panicles later than *B. japonicus*, yet all three matured earlier than the latter species (Fig. 4).

The same phenological relationships among species were observed in the field as in the row plantings.

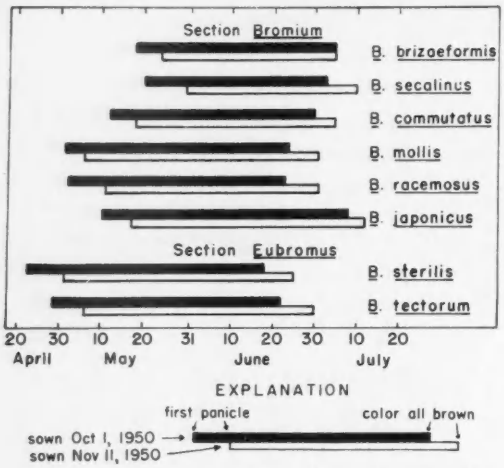

FIG. 4. Phenology of species of *Bromus* in row plantings at Lewiston Study Area grown from seed collected in the Columbia Basin.

No useful data were obtained in the plantings for *B. rubens* and *B. rigidus* because of the winter injury, but field observations indicated that they, like the other species in the section Eubromus, are early in maturity. The species in the section Bromium generally mature later than the species in the section Eubromus.

ROOT STUDIES

Field workers have generally assumed that *Bromus tectorum* is a shallow-rooted grass. Tisdale (1947) says: "Dwarf, early maturing species such as *Poa secunda* and *Bromus tectorum* have shallow root systems which rarely penetrate below a depth of one foot." H. C. Hanson (1950) writes: "In spite of its shallow root system, *Bromus tectorum* has been able to invade and compete successfully with shrubs and deep-rooted perennial grasses. In Utah, for example, its roots penetrate to only about six inches, while those of the perennial *Agropyron inerme* and *Helianthella uniflora* reach four and five feet, respectively." This statement is based on work by W. R. Hanson & Stoddard (1940) in Utah. In their paper the only reference to *B. tectorum* is a figure of a bisect in a climax stand of *Agropyron inerme* showing two plants of *B. tectorum* whose roots are confined to the top 6 in. (15 cm) of the soil. The root systems of the plants were studied by using an ice pick to separate the soil from the roots.

Spence (1937) studied the root systems of the important plants in the Boise River watershed in southwestern Idaho by digging a trench and then using an ice pick to separate soil from the roots. He found that *B. tectorum* produced an average of 7 roots per plant and that these penetrated an average depth of 30 cm (1 ft). In contrast, the long-lived perennial grass, *Agropyron inerme*, produced 176 roots per plant and these penetrated 105 cm (3.5 ft).

Three main methods were used in the present study of root systems of *Bromus tectorum*: (1) washing out root systems with water, (2) insertion of lithium chloride into the soil and later spectroscopically analyzing tops for the presence of lithium; this and the first method gave data on extent of the root systems, and (3) collection of volume samples of soil in a pure stand of grass, washing out the roots, drying, and weighing; this is a quantitative method.

The first method was modified in two ways. For young plants, columns of soil containing the entire root system were obtained. After thorough soaking of the column, the soil was slowly washed away from

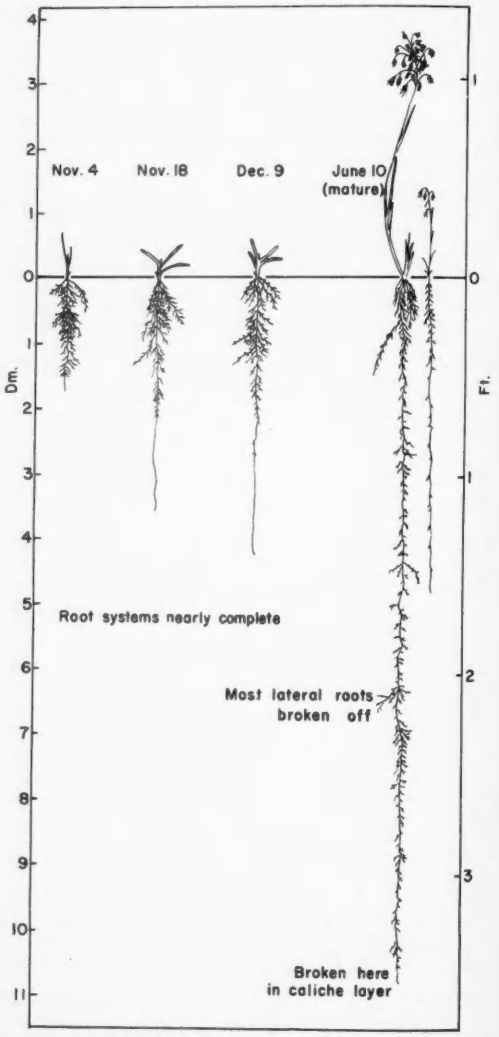

FIG. 5. Development of *Bromus tectorum* in pure natural stands at the Lewiston Study Area, 1951. Germination occurred Oct. 5. Large plant sampled on June 10 was typical of dominant plants; the small one was a stunted plant in same stand. Because roots were dense near the surface it was not ascertained if there was more than one long root on the large plant.

the roots with a fine spray of water. This method is much like that described by Pavlychenko (1937) but on a smaller scale. The root systems shown in Fig. 5 of plants in November and December were obtained in this way.

Roots of mature plants extended so deep that it was not possible with the available equipment to obtain columns of soil containing whole root systems. Instead a pit was dug and the roots washed out of the face of the pit, in a manner described by several workers, including Stoeckeler & Kluender (1938). Washing was done with a spray of water from a two-gallon pressure tank garden sprayer. The long roots were found to be so nearly straight and vertical that it was important to use a carpenter's level to make a vertical face on the side of the pit before beginning washing. Using this method the deeper roots were followed into the caliche layer, the upper limit of which was about 1.2 m (4 ft) below the surface (Fig. 5). The cementing of the soil particles was so strong below this depth that washing was ineffective. Whole root systems were not obtained, but individual roots were traced into the caliche layer in three different profiles by this method. Roots so obtained were preserved by floating them onto a long strip of paper while in a tank of water (Pavlychenko 1937). After drying, the roots were held in place by spraying on a coat of plasic. Roots were found to be very abundant in the top 2 to 3 dm of soil, becoming gradually sparser in the deeper layers.

The first method requires many hours of work for deep root systems, and is not useful for studying the long delicate roots of annual bromegrasses in mixed stands of grasses. Because tracer techniques should not have these disadvantages, the lithium chloride tracer method, modified from that described by Sayre & Morris (1940), was employed. A hole was made in the soil with a King tube at an angle of 30° from the vertical, thereby not disturbing the roots which would grow into the soil containing the lithium. The empty King tube was reinserted into the hole to a depth of a few centimeters from the bottom. Through a piece of flexible tubing inserted in the King tube, 5 ml of a solution of lithium chloride (0.2 gm LiCl per ml) was poured into the bottom of the hole followed by a few milliliters of distilled water for a rinse. These precautions were employed to prevent the contamination of shallower layers of the soil when removing the tubes. Finally soil was packed firmly in the hole to replace that removed. One to 12 weeks later tops of the plants directly above the lithium were collected. After ashing in a flame, these samples were analyzed spectroscopically for the presence of lithium. The analyses, recorded photographically, were made by arcing the samples at 9 amperes, 310 volts for one minute, using high purity carbon electrodes, by the Spectroscopic Analysis Laboratory of the Institute of Technology at the State College of Washington.

In a trial series results were encouraging. Although the control sample showed a slight amount of lithium, samples suspected of having roots at the necessary depth showed distinctly higher contents of lithium. In later tests, however, some controls were found to have a content of lithium as high as some plants known to have roots as deep as the lithium in the soil below them. Therefore only the few cases in which test plants had markedly higher contents of lithium than any control were considered reliable.

The results indicate that roots of *Bromus tectorum* picked up lithium from the following depths: (1) at 7.5 and 10 dm in two different native grasslands of the *Festuca/Agropyron* Association (Daubenmire 1942) on silty-clay loam soil, (2) at 7.5 and 10 dm depths at the Lewiston Study Area in a natural stand of *B. tectorum,* and (3) at 20 dm (5 dm into the caliche layer) at the Lewiston Study Area in an artificially planted plot with about 20 plants per sq dm. Roots of *B. tectorum* in natural stands were found, on the basis of 18 tests, to extend laterally 20 to 30 cm at 1, 2 and 3 dm depths in the Lewiston Study Area.

Judging by the results of the first method, it is believed that all these data from the lithium method are less than the maximum extent of the roots of the plants tested except for the one test at a depth of 2 m. It was not expected that roots of *B. tectorum* would penetrate the caliche layer to that extent. However, since the washing method showed that the roots entered this hard layer, the lithium test suggesting penetration 5 dm into the caliche layer does not seem unreasonable.

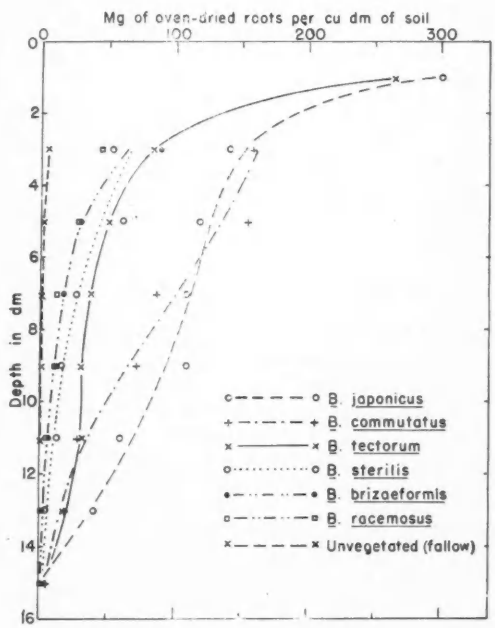

FIG. 6. Relation of root weights of mature Bromus plants to soil depth in row plots at the Lewiston Study Area, June 23-25, 1951. Points represent single determinations except for *B. japonicus* and *B. tectorum,* which are averages of 2 and 3 determinations, respectively.

The third method involved using an orchard auger to obtain samples of soil of a known volume (80 mm in diameter and 2 dm deep) in pure stands of the grass. Samples were placed on a fine mesh wire sieve and the soil washed through with a fine spray of water. Foreign matter, mostly dead organic matter, was sorted out and the roots then oven-dried at 105°C and weighed. Usually the sample from 0 to 2 dm was discarded because the high organic matter content made it extremely difficult and time consuming to obtain clean roots. One check on the method was made by collecting samples from an area kept free of *B. tectorum* and other plants for one year. The results (Fig. 6) indicate that no appreciable error was present due to old roots or other extraneous material in the soil.

The weights of roots of 6 species at maturity in row plots at the Lewiston Study Area are given below. For each species the first value is the total weight of oven-dry roots per sq dm of soil surface area, and the second is a relative rating calculated as a percentage of the production of *B. tectorum*.

B. japonicus	.603 mg	232%
B. commutatus	.526	203
B. tectorum	.259	100
B. sterilis	.174	67
B. brizaeformis	.162	63
B. racemosus	.107	45

The values for *B. japonicus* are averages of three determinations, for *B. tectorum* two, and for the others one determination. The accuracy may be only within 25%, but the lack of overlap between the replicates of *B. tectorum* and those of *B. japonicus* supports the validity of the results. In addition to the total weight of roots produced by these species, a comparison of their weights at various depths is shown in Fig. 6. All produced roots to the same depth of 15 dm, but *B. japonicus* had a greater proportion of roots at the 8-14 dm depths than the others.

Fourteen determinations of root weight were made in a series of plots at the Lewiston Study Area in which *Bromus tectorum* had been planted at 4 densities. The first set of these plantings was made in the early fall (Oct. 7, 1950) and another series in the late fall (Nov. 11). Root development at maturity was not significantly different in the late fall plantings from that in the early fall plantings. Since early fall plantings began growth earlier and matured earlier than late fall plantings, there was a small difference when sampled at the same calendar date. Root development was only a little less in the sparsest (av 0.75 plants per sq dm) than in the densest (av 25 per sq dm) plots (Fig. 7).

The addition of ammonium nitrate at rates of 3.6 and 7.2 gm of nitrogen per sq m (80 lb/A) to natural stands of *B. tectorum* resulted in striking increases in the weights of the roots of *B. tectorum*. The oven-dry weight of roots in a vertical column of soil 1 sq dm in surface area was 1320 mg in the heavily fertilized plot compared to 540 mg in the control plot, a difference of 240%. Even more striking than the increase in total weight is the increase in the 8 to 12 dm depths, where the fertilized plants produced over 6 times as many roots by weight as unfertilized plants (Fig. 8). This increased root growth in the nitrogen-fertilized plots appears to be correlated with the conditions of the shoots during late April after 6 weeks without precipitation. At that time the plants in the unfertilized plot were stunted and had a purplish-brown cast; those in the heavily fertilized plot were 3 times as tall and bright green. The added nitrogen apparently allowed the plants to produce root systems adequate for securing water from the deeper layers at a rate sufficient to maintain rapid growth. The soil moisture data support this assumption, as the soil moisture was depleted to a greater depth in the fertilized than unfertilized plots. Perhaps in a moister spring the effect of nitrogen fertilization would be less because of greater release of available nitrogen through decay of organic matter, possibly by increased bacterial nitrogen fixation, and because of the less critical water relations.

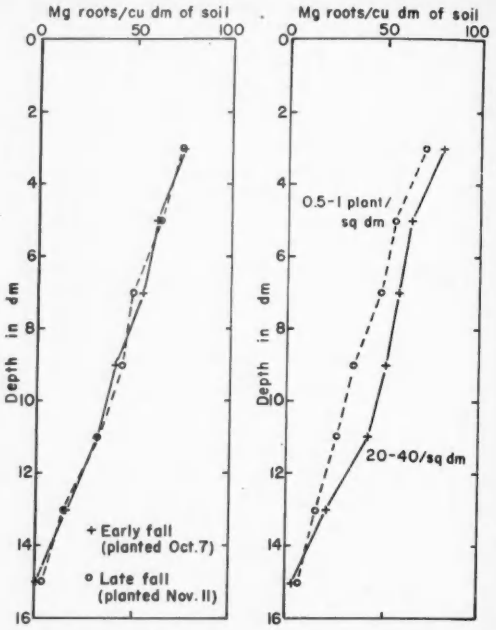

FIG. 7. Relation of planting date (left) and density (right) to root development of mature *Bromus tectorum* in experimental plots at the Lewiston Study Area. Points in graph on left represent averages of equal numbers of sparse and dense plots.

Roots of *B. tectorum* were found to extend deeper than was expected. Root depth undoubtedly varies with soil type, climate, grazing, and other factors. Nevertheless, it seems likely that the disparity in root depths obtained by the writer and by others is explained more by differences in methods employed than in environmental causes. Even the main roots of *B.*

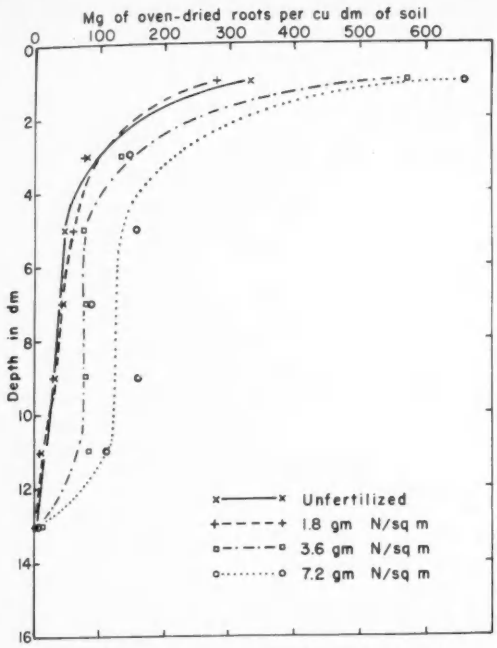

FIG. 8. Influence of ammonium nitrate fertilization on root development of *Bromus tectorum* in pure natural stands at Lewiston Study Area. Sampled at maturity in June, 1951.

tectorum were found to be small and fragile, much more easily broken than roots of perennial grasses like *Agropyron spicatum*. Experience suggests that such fine roots would be extremely difficult, if not impossible, to accurately trace very far using the ice pick method. Even the use of a fine spray of water to wash out the roots often resulted in breakage when small lumps of soil resistant to erosion were freed by removal of the surrounding soil. It is probable that only the very dense portion of the root system has been detected by those using the ice pick method on *B. tectorum*.

SOIL MOISTURE STUDIES

A King type soil tube, modified in a manner similar to the recommendations of Veihmeyer (1929), was used for most soil sampling for moisture determination. Percentages are based on the oven-dry (105°C) weight of the soil.

Determinations of soil moisture at permanent wilting were made by growing one sunflower (*Helianthus annuus*) and two wheat (*Triticum aestivum*) plants in the soil in glass tumblers in the greenhouse. Wheat, because of its finely divided root system, was used to help give as even utilization of the water as possible, and the sunflower served as the more obvious indicator of wilting. The tumblers were kept in a large pan of water to reduce the rate of temperature change. A layer of sand 1 cm deep was placed on the soil in each tumbler to reduce evaporation. Permanent wilting was considered to be reached when the first true leaves of the sunflower were wilted and did not regain turgor when covered overnight by a bell jar. The soil in the bottom half of the tumbler was then used for determining soil moisture by weighing and oven-drying. The conspicuous roots, chiefly on the outside of the soil mass, were removed, but the small roots not easily seen within the soil were left in place both because it would be impossible to quickly remove them and also to be comparable to field samples in which such small rootlets are present. In Table 9 are given the values of the permanent wilting percentage of soil samples at the Lewiston Study Area, and the corresponding values of the moisture content on a volume basis.

TABLE 9. Moisture content at permanent wilting in soil samples from the Lewiston Study Area. Values given are averages of two or more tests of samples from each of three locations in the Study Area.

Depth dm	Permanent wilting percentage (dry wt basis)	Volume-weight of oven-dry soil, dm/cc	Water content at permanent wilting gm/cu dm
0-1	7.9	1.30	103
1-2	7.8	1.38	108
2-4	7.6	1.42	108
4-6	7.5	1.42	106
6-8	6.2	1.42	87
8-10	5.9	1.48	87
10-12	5.9	1.48	87
12-14	5.1	1.48	75
14-16	4.2	1.48	62

In the field the actual soil moisture was found in a few cases to be reduced, in the deeper soil where evaporation is negligible, to values distinctly below the moisture content at permanent wilting as determined in the greenhouse. This difference amounted to 1-2% by weight for much of the root zone in the heavily nitrogen-fertilized plot of *B. tectorum* (Fig. 11). The range in values obtained in the greenhouse determinations of permanent wilting percentage did not include these low values found in the field. Therefore it did not seem wise to assume that variation in the soil was an adquate explanation, even though possible. Briggs & Shantz (1912) showed clearly that plants can continue to extract water below the value at permanent wilting if all the root zone is in soil at or below the permanent wilting percentage. In the field the plants which had reduced the soil moisture below the wilting percentage in the mid-portion of their root zone had roots in deeper soil where available water was present and the plants were still actively growing. Breazeale (1930), Breazeale & Crider (1934), and Breazeale & McGeorge (1949) report that plants do not reduce soil moisture below the value at permanent wilting if part of the root system is in soil with an ample moisture supply.

Considering these things, it seemed wise to check on the determinations of permanent wilting percentage to see if they were in error. To check on the

effect of soil structure, soil samples were obtained in an undisturbed structural condition by carefully forcing cans into the soil with an hydraulic jack and then ascertaining the permanent wilting percentage by growing plants in the soil samples in these cans. The results (Table 10) indicate similar soil moisture values in disturbed and undisturbed soil.

TABLE 10. Permanent wilting percentage in soil samples with natural structure compared to that in disturbed soil samples from the Lewiston Study Area.

1-2 DM DEPTH		1 METER DEPTH	
Natural	Disturbed	Natural	Disturbed
7.6	7.8	6.6	6.9
7.6	7.6	7.0	6.5
8.2	7.7	6.4	6.4
7.4	7.9	6.6	6.5
7.1	7.8		
Mean 7.58	7.76	6.65	6.58

To see if the plant species involved affected the value, *Bromus tectorum* was used in place of wheat, along with sunflower, in some trials. Using *B. tectorum,* the results averaged 0.2% lower than when using wheat, but there was overlap in the values. The results do not warrant concluding that a real difference exists in ability to extract water. Since sunflower was used as the indicator of wilting in both series, no large differences are to be expected.

These greenhouse tests of the permanent wilting percentage do not explain the discrepancy between the values originally obtained in the greenhouse and in the field plots. Further study is being given this subject.

On April 5 the soil moisture supply in the Lewiston Study Area plots planted at various densities of *Bromus tectorum* was nearly as great as in bare plots. During the rest of the growing period the soil moisture was steadily depleted by the plants as shown in Fig. 9. These data show clearly that with the advance of the season the available water was removed from successively deeper portions of the soil. On May 17, when inflorescences were green and the plants not fully grown, the most densely planted plots were a little drier than the most sparsely planted plots but by July 6, when all plants were mature, the soil moisture was the same in all plots (Fig. 10). These facts apparently are related to the observation that the plants in the sparse plots continued to grow and were greener longer than in the dense plots.

Natural stands of *B. tectorum* were fertilized with ammonium nitrate. As in the previous case, the plants utilized soil moisture at increasingly greater depths as the season advanced (Fig. 11). On April 22 inflorescences were small and inconspicuous; on June 8 the plants were mature and beginning to dry.

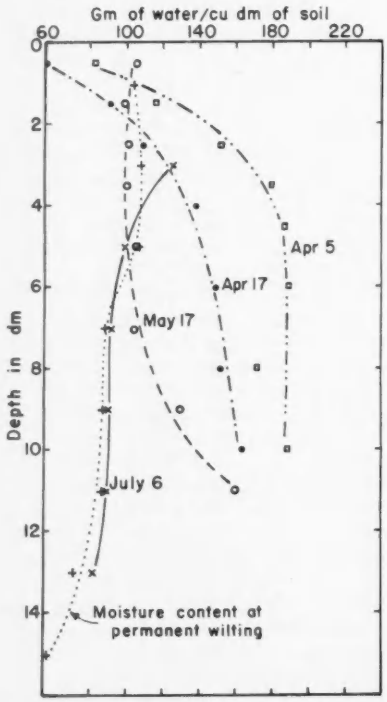

FIG. 9. Reduction in soil moisture with advance of the season in the densest (20 plants per sq dm) early fall plantings (Oct. 7, 1950) at Lewiston Study Area, 1951. A rain on July 4 wetted the upper 3 dm.

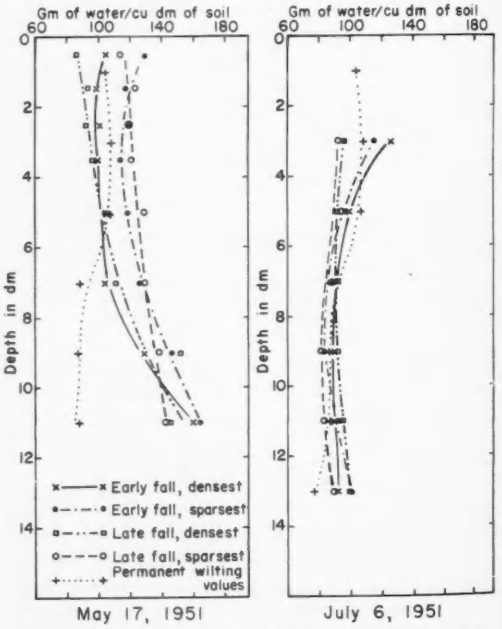

FIG. 10. Soil moisture in relation to density and planting date of *Bromus tectorum* at Lewiston Study Area. On May 17 all were green; on July 6 all dead. Densest early fall planting (Oct. 7, 20-40 /sq dm) was most advanced and the sparsest late fall planting (Nov. 11, 0.5-1 /sq dm) least advanced during the growing period.

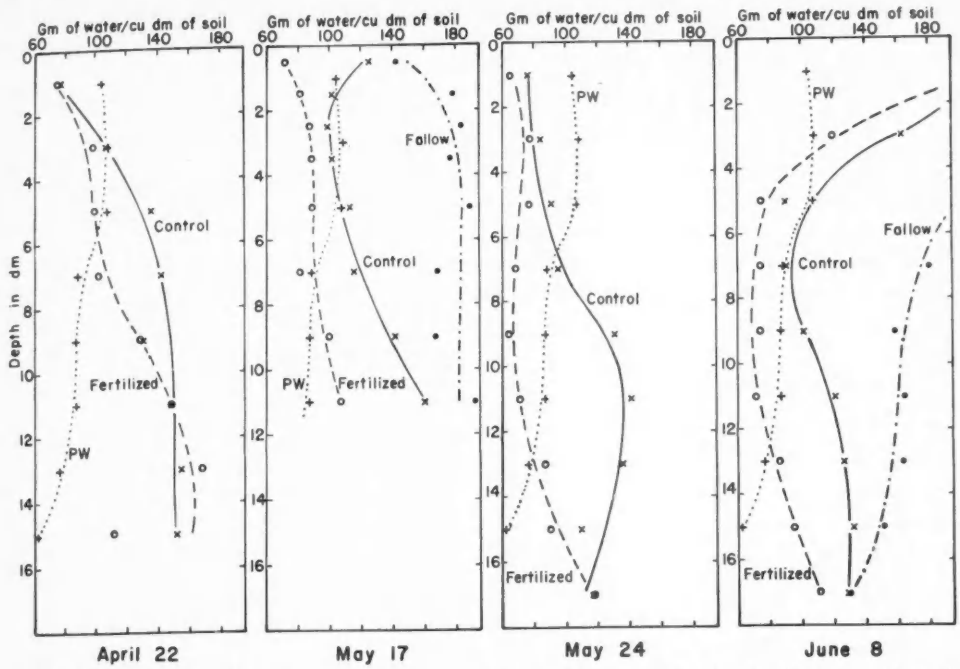

FIG. 11. Changes in soil moisture under nitrogen fertilized (7.2 gm/sq m) and unfertilized natural stands of *Bromus tectorum* at Lewiston Study Area, 1951. On April 22 plants green and without panicles; on June 8 mature and brown. Moisture content in unvegetated plot (fallow) and moisture content at permanent wilting (PW) given for comparison. A rain on July 4 wetted the upper 3-4 dm.

Heavily fertilized plants (7.2 gm of N per sq dm) utilized much more water than did the unfertilized plants (controls). From the middle of March to the last of April no precipitation was received sufficient to wet the soil. The unfertilized plants, only 2 to 3 cm high, developed a purplish-brown cast during late April, while the fertilized plants, 6 to 16 cm high, remained conspicuously green. It seems certain that this difference in utilization of soil water is related to the fact that the fertilized plants had a greater amount of roots, especially at the greater depths, than did the unfertilized plants (Fig. 8). The unfertilized plants did not become stunted due to a lack of available soil moisture but due to a lack of sufficient root growth to obtain the water in the deeper layers.

A rough estimate of the water use per *B. tectorum* plant was obtained as follows. In natural stands at the Lewiston Study Area the density averaged about 100 per sq dm in 1951. The yearly precipitation provided a total of 35 gm of water per plant, which would be reduced appreciably by evaporation from the soil, and perhaps slightly by runoff or percolation. The soil moisture determinations showed that in the depths of 4-16 dm, which is below the layer affected by evaporation, each unfertilized plant extracted 4.0 gm and each heavily fertilized plant extracted 5.9 gm of water from March 15 to June 8. Since this excluded use in the 0-4 dm layer and use before March 15, the actual amounts used would be distinctly higher, perhaps between 15 and 25 gm per plant. On the average each unfertilized plant was 10-15 cm high and the top weighed 0.02 gm oven-dry; each fertilized plant was 35-45 cm high and weighed 0.07 gm. Thus it seems probable that the fertilized plants produced more weight per gram of water used than the unfertilized plants.

EFFECT OF DATE OF PLANTING ON FLOWERING

Of the 10 species studied, only *B. rubens* flowered normally without being subjected to cold temperatures. Under natural conditions these plants usually germinate in the autumn and so receive the necessary cold temperatures during the winter. If planted after a certain time in the spring, however, they will flower feebly if at all. Beddows (1931) noticed this in *B. tectorum* but did not relate the observation to cold requirement. He wrote:

> *Bromus tectorum* is always described as an annual. It is, therefore interesting to note that seed . . . sown on February 29th, 1928, developed no panicles during that year. These plants made a dense, leafy growth during the summer, fell off badly in the autumn, but survived the winter, sending up an abundance of panicles in May, 1929.

After studying the effect of date of planting on flower production in *B. tectorum* and *B. commutatus* in Nebraska, Finnerty (1951) wrote:

Plants from seed sown in the field prior to March 1 consistently head and set seed in the late spring or early summer of the same year in which they are sown. Plants from seed sown after March 1, but before April 1, usually set seed in the current year, although heading is sparse, occurring mostly in July. Most seeds sown after April 1 normally do not produce plants heading and maturing seed in the same year. However, a few scattered small panicles have been observed emerging in August from plantings made in early April of the same year. Many of the plants overwinter and head the following year although considerable winterkilling occurs. It appears that April 1 approaches the critical germination date for both species. Vernalized seed of either species, even when planted after April 1, gives rise to plants which head normally. In one test downy brome [*B. tectorum*] and Hairy chess [*B. commutatus*] plants grown from seed vernalized 24 days at 3°C. and planted outside on April 3 had headed by June 30th of the same year.

G. W. Fischer, State College of Washington, and L. R. Schwendiman, Soil Conservation Service, both told the writer of observing a lack of flowering in *B. tectorum* when spring planted at Pullman, Washington.

Row plantings of the collections of *B. tectorum* from various localities were made at the Lewiston Study Area on April 2, 1951 and at the Pullman Study Area on April 4. Because of drought at both areas, only rare individuals germinated until after a rain on April 28. At the Lewiston Study Area three inflorescences had been produced by August 9, one on plants grown from seed collected at Pullman, the other two from Umatilla County, Oregon. All these spring plantings died in August, most likely due to drought. At the Pullman Study Area a few panicles were produced in 23 out of 28 spring-planted plots, but the number was always only a small fraction of the number produced in fall plantings (Fig. 12). In 5 plots the plants produced 20-60 inflorescences which is about 1-3% of the production in fall plantings. The seed for these 5 plots came from (1) Umatilla County, Oregon, (2) Morrow County, Oregon, (3) Reno, Nevada, and (4 & 5) Pullman, Washington (2 collections). The spring planting of seed from Israel (Fig. 12) produced more inflorescences than any collection from North America, but even in this case the number was small. Because the fall plantings of Israel seed winterkilled, no comparison between the flowering of fall and spring plantings is possible.

Samples of a local collection of *B. tectorum* were planted at the Lewiston Study Area on February 24, March 24, April 5, and May 4, 1951. The April 5 planting germinated at the end of April; the others germinated promptly. Those planted Feburary 24 began to produce panicles in normal numbers on June 2, but the others produced only rosettes which died later in the summer.

Of the other species of *Bromus* studied, none produced panicles in normal numbers in the spring plantings at the Lewiston Study Area. These plants died in late July or August, presumably due to drought. The number of inflorescences produced in the spring plantings at the Pullman Study Area (which germinated in late April) expressed as an estimated percentage of the number produced in the fall planted plots, are as follows:

FIG. 12. Flowering of *Bromus tectorum* from Montana (foreground plot) and Israel (second plot) in spring plantings at Pullman Study Area, Aug. 4, 1951. Seed sown April 4; germination mostly at end of April. Fall sown plants produced many more panicles.

B. brizaeformis	0
B. commutatus	C—Trace (2 panicles in 1 of 3 plots)
B. japonicus	T—2
B. mollis	0
B. racemosus	0
B. rigidus	5
B. rubens	Flowered abundantly
B. secalinus	0
B. sterilis	Trace (1 panicle)
B. tectorum	O—3 (N. Amer. collections)

No percentage figure is given for *B. rubens* because it winterkilled in the fall plantings, as did the Jerusalem collection of *B. tectorum*.

These results indicate that all species except *B. rubens* need a cold treatment if flowering is to be normal. The absence of panicles on the spring planting of *B. rubens* at the Lewiston Study Area may indicate that even this species needs some cool temperatures if flowering is to be normal. The absence of flowering may be due, however, to a deficiency in soil moisture for good growth during the summer. One reason for this interpretation is that in greenhouse tests *B. rubens* produced numerous panicles containing viable seeds, but other species produced very few or none.

TIME OF FLOWERING IN RELATION TO PANICLE GROWTH

Stage of development of the florets was observed daily in relation to the growth of the inflorescences on 4 plants of *B. tectorum* growing under moderately favorable conditions at Pullman, Washington, in 1950. Measurements were made for 28 days until terminated due to mowing of the plants. The distances from the crown of the plant to each of the following were measured: (1) collar of uppermost leaf sheath, (2) tip of the inflorescence when stretched out in a straight line, (3) base of the inflorescence, taken as the junction of the main axis with the lowest branch of the panicle. The results for one inflorescence, shown in Fig. 13, were in agreement with the results in the other three inflorescences.

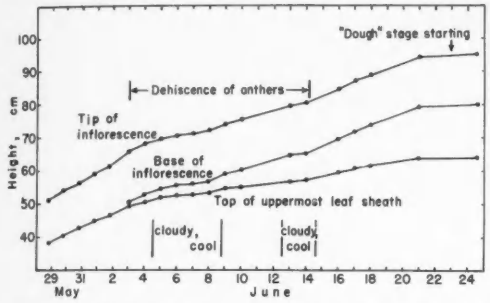

FIG. 13. Relationship of height growth of an inflorescence of *Bromus tectorum* to flower and fruit development. Pullman, Washington, 1950.

The stages could be dated only approximately because the uppermost spikelets on a branch were further advanced in development than the lower ones, and within a spikelet the lowest floret was the most advanced. Some florets shed pollen before the bottom of the panicle had emerged from the sheath and dehiscence of the anthers continued for at least ten days in other spikelets of the inflorescence. Starch accumulation had proceeded to the "dough" stage in the ovaries of the older florets about 20 days after anthesis began. By that time elongation of the inflorescences, which were still entirely green, seemed to have nearly ceased.

SHOOT AND SEED PRODUCTION OF *Bromus tectorum*

Shoot and seed production was determined in the series of plots planted at 4 densities in the early fall (Oct. 1, 1950) and late fall (Nov. 11) at the Lewiston Study Area (Fig. 14). At maturity the shoot systems were clipped at a height of 1 cm from 2 x 5 dm areas in each plot to obtain yield data. The number of plants was counted when possible, but in some cases crowns were so clustered it was impossible to distinguish individuals. In the laboratory the following were determined: oven-dry (105°C) weight of shoot systems (including florets), number of culms, number and air-dry weight of florets (seeds), and number of spikelets in both smutted and non-smutted inflorescences. At least 500 florets in each sample were counted and weighed, and the total number

FIG. 14. Development of *Bromus tectorum* in relation to density and planting date, Lewiston Study Area, May 15, 1951. Decimeter marked stake is in an early fall planting (Oct. 7) at greatest density; plot to lower right is a late fall planting (Nov. 11) at greatest density.

then calculated using these data plus the total weight of florets. In many samples of 500 to 1000 florets the mean weight of one floret, air-dry, was 2.5 to 3.7 mg, which is equivalent to 270 to 400 florets per gram or 125,000 to 180,000 florets (seeds) per pound.

Smutted inflorescences and culms appeared to be developed to the same size as non-smutted culms. Therefore shoot weights were not corrected for smutting. To compare floret production in different plots, compensation for the influence of smut was made by assuming that smutted panicles would have produced as many seeds per spikelet as non-smutted ones if the smut had been absent. There seemed to be no reduction in numbers of spikelets due to the smut, so this semed like a valid assumption.

The data on production at the four densities and two planting dates (Fig. 15) indicate that:

(1) The total weight of shoots per unit area varied little, ranging from 4 to 6 gm per sq dm. There is an indication that peak production was in the range from 1 to 5 plants per sq dm, a lower density than usually found in pure natural stands in the Lewiston area.

(2) The number of seeds produced per unit area varied with density much as did shoot weight, but showed a more pronounced reduction at high densities.

(3) The number of culms per plant increased markedly (from 1.9 to 13.3) with a decrease in the number of plants per unit area (from 19.7 to 0.6 plants per sq dm), but in spite of the larger number of culms per plant in sparse plots, the number of culms per sq dm was less in the sparsest (8 per sq dm) than in the densest plots (37 per sq dm).

(4) Weight per culm, weight per plant, number of seeds per culm and number of seeds per plant decreased with increasing density.

These results, indicating a tendency for uniform production over medium density ranges but decreasing production at high densities, agree with the find-

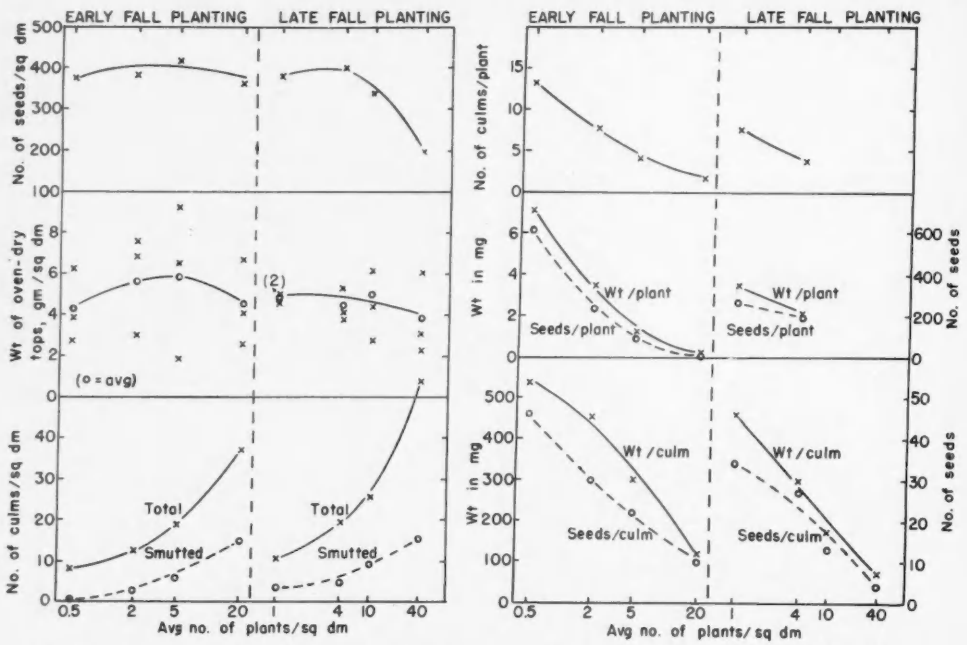

FIG. 15. Shoot and seed production of mature *Bromus tectorum* in the density plots, Lewiston Study Area, 1951. Correction in seed number was made for smutting as indicated in text. Density scale is logarithmic.

ings of Salisbury (1942) who observed that adverse conditions reduce the quantity of seeds per plant but not the quality. On the basis of studies by himself and others he concluded that below a certain density increased production per individual does not compensate for the decreased number per unit area, and above a certain density increased numbers per unit area do not compensate for the decreased production of the depauperate plants.

The results obtained on the density plots at the Lewiston Study Area give possible support to the findings of Piemeisel (1951) of cyclic changes in density of *B. tectorum* in fields in southern Idaho abandoned from cultivation and subsequently undisturbed. He reported an increase in successive years from a very low to a very high density, accompanied by a sharp reduction in seed yield, due to the very high density, the last year of each wave of the cycle. The densities in the studies reported here were much less than the densities occurring the last year of the reported cycles, but there is an indication that seed production per unit area did decrease when density increased above the optimum of about 5 plants per sq dm. This is evident in the late fall planted series (Fig. 15) in which greater densities were obtained than in the early fall series. It is important to remember, however, that *B. tectorum* plants can produce one seed when so severely stunted that they are only 4 to 5 cm high. Such plants are indeed inconspicuous.

Shoot and seed production was studied also in nitrogen fertilized plots artificially planted to two densities at the Lewiston Study Area. The land did not lie fallow the summer previous to planting as did the land for the plots reported earlier (which were unfertilized). On one plot of each density ammonium nitrate was broadcast on October 15, 1950 at rates supplying 0, 1.8, 3.6 and 7.2 gm of nitrogen per sq m (0, 20, 40, and 80 lbs per A). The Bromus seed was broadcast on October 21. The results (Fig. 16) indicate:

(1) The number of plants per unit area was twice as great in the heavily fertilized as in the unfertilized plot. Because the rate of seeding was constant for all rates of fertilization, this increase is presumed to result from reduced mortality.

(2) The number of culms per unit area was 230% greater in the heavily fertilized than in the unfertilized plot due mostly to the increased number of plants per unit area and slightly to an increase of about 20% in the number of culms per plant.

(3) The weight of oven-dry tops increased 2 to 3 times and the number of seeds per unit area increased 2 to 3.5 times with an increase in the rate of nitrogen fertilization. The greater increase occurred in the dense series.

An additional group of plots received an application of phosphorus fertilizer, but no effect on size or time of maturity was noticed.

A third series of shoot and seed production data were obtained on natural stands of *B. tectorum* at the Lewiston Study Area which were fertilized with ammonium nitrate at the same rates as in the artificially planted plots just described. The nitrogen fertilizer

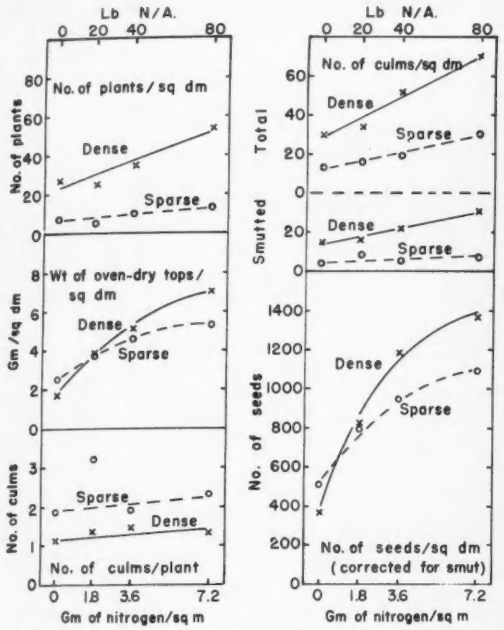

FIG. 16. Shoot and seed production of mature *Bromus tectorum* on nitrogen fertilized plots cultivated and planted sparsely and densely, Lewiston Study Area, 1951.

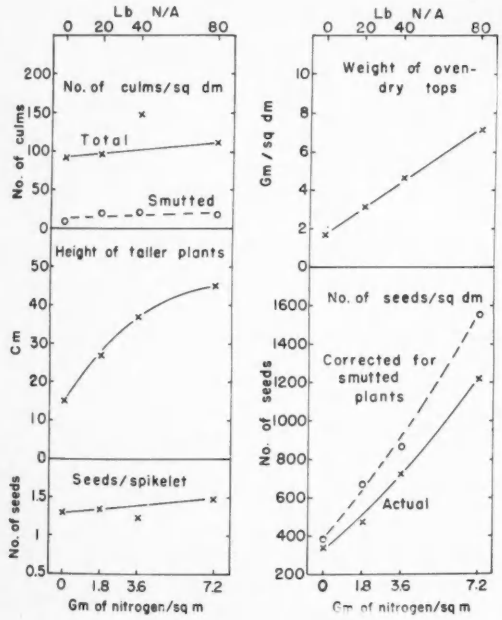

FIG. 17. Influence of nitrogen, applied as ammonium nitrate, on shoot and seed production at maturity on plots in natural *Bromus tectorum* stands, Lewiston Study Area, 1951.

FIG. 18. Effects on April 21 (top) and on May 15, 1951 (bottom) of ammonium nitrate on growth of *Bromus tectorum* in a natural stand at Lewiston Study Area. Foreground plot unfertilized, rear plot received 7.2 gm nitrogen per sq m (80 lb/A) on Oct. 15, 1950.

was broadcast evenly on the plots on October 15, 1950, a few days after germination of *B. tectorum*. The density in these natural stands was about 100 plants per sq dm, which was two to three times the density in the dense plots of the artificially planted and fertilized series. Probably the higher density accounted for the more pronounced effect of nitrogen fertilization in these plots (Fig. 17) than in the ones artificially planted. Differences in size of the fertilized and control plots was evident within a few weeks after fertilization, and increased up to maturity (Fig. 18). The oven-dry weights of shoots per sq dm were very similar to the production in the dense series of artificially planted plots, increasing from 1.65 gm when unfertilized to 7.2 gm (increase 435%) in the plot receiving 7.2 gm of nitrogen per sq m. Seed production was four times greater at this heavy rate of fertilization than when unfertilized.

The effect of nitrogen fertilization on shoot growth was greater than the effect on root growth. In heavily fertilized plots the oven-dry weights of the shoots was 435% greater and of the roots 240%

greater (see earlier discussion) than in unfertilized stands.

These shoot production rates for *B. tectorum* at the Lewiston Study Area agree well with the results reported by Hull & Pechanec (1947) for air-dry forage production on four different areas in the Snake River Plains of southern Idaho in the years 1940-46. They reported productions of 441 to 3461 pounds per acre (0.5 to 4 gm per sq dm). At the Lewiston Study Area the production of oven-dried shoots ranged from 1.6 gm per sq dm for unfertilized stands to 7.2 gm in stands fertilized with 7.2 gm of nitrogen per sq m.

MOISTURE CONTENT OF SHOOT SYSTEMS

Shoot systems of *B. tectorum* plants at the Lewiston Study Area were clipped at 2 to 3 cm above the soil surface, enclosed in soil cans, and taken to the laboratory, where fresh and oven-dry (105°C) weights were obtained. The results (Table 11) indicate that there was a progressive reduction in moisture content of the shoot systems from the time inflorescences developed until the plants became entirely brown. When the plants developed a conspicuous purple color the moisture content was about 0.6 that of the vegetative plants; when the plants first became all brown the water content was about 0.4 that of vegetative plants but still 5 to 6 times that of air-dry shoots stored in a laboratory.

TABLE 11. Moisture content (% of fresh wt) of shoot systems of *Bromus tectorum* at different stages of development. Samples collected at Lewiston Study Area unless otherwise stated.

Date collected	Per cent moisture	Stage of development
1950		
April 9	72, 76	Well-tillered vegetative bunches (samples from the Pullman Study Area)
May 6	70	Inflorescences just emerging from sheath
May 6	68, 68, 66	Inflorescences emerged completely, but stalks not fully elongate. Shedding of pollen occurring or just finished
May 13	68, 65	Inflorescences green, stalks about mature size, ovaries large and juicy
May 20	62, 62, 61	Ditto
May 27	60	Ditto
May 27	61, 60	Ovaries starchy (doughy), otherwise look like previous ones
June 3	58	Plants tall and green; ovaries starchy
June 3	47	Stems, awns, and glumes purple, lemmas purple or green
June 10	44	Parts of glumes and lemmas brown, mostly purple
June 3	30	Plants dry; leaves, stems, glumes, lemmas, and paleas light brown; ovary purplish-brown
June 10	23	Plants brown, ovaries not all dry
1952		
January	4-6	Air-dry tops stored in paper sacks in laboratory at Minneapolis, Minnesota (7 samples tested)

EFFECT OF CLIPPING ON *Bromus tectorum*

A series of plots 70 cm on a side were planted Oct. 7, 1950 at the Lewiston Study Area at rates resulting in densities of 5 to 10 plants per sq dm. The plants on 6 plots were clipped once, 2 plots being clipped on each of the following dates: April 21, May 12, and May 24, 1951. These plots were otherwise undisturbed.

On April 21 inflorescences were starting to emerge from the sheaths at the time of clipping. New culms were subsequently produced which were a few days behind, in stage of development, and only slightly shorter in height than the unclipped plants.

In the plots clipped May 12, inflorescences were nearly full size, but they were still green and anthesis was incomplete at the time of clipping. New inflorescences emerged 3 to 4 weeks after clipping and later attained one-half the height of those on unclipped plants. On June 15 when inflorescences on unclipped plants had become brown, those on the clipped plants were mostly green with a little purple coloration.

On May 24 plants had attained full size and were 99% green and 1% purple when clipped. The ovaries were large and in the "dough" stage. On this plot all plants were killed except for one on the border of the plot adjacent to a bare area. In other plots it was found that plants matured earlier in dense stands than in sparse stands, so that the plant adjacent to the bare area that survived clipping may have been less advanced in stage of development than others in the plot. In general the results of these clipping tests indicate that the possibility of regeneration following clipping decreases as the plants advance in development through flowering to fruiting.

One plot at the Lewiston Study Area was clipped 5 times at a height of about 2 cm. The weights of tops obtained were as follows (accuracy ± 10%):

	Fresh weight	Oven-dry weight
April 21	400 gm/sq m	100 gm/sq m
May 12	350	90
May 24	80	20
June 9	20	7 (estimate)
June 23	16	5
Total	866	222

On June 23 many plants were dead or dying. Those still growing had produced inflorescences successively shorter and smaller with each clipping. No purple coloration developed on the surviving plants by June 23.

On unclipped plots of about the same density (5 plants per sq dm) the oven-dry shoot production at maturity amounted to about 500 gm per sq m. One test is insufficient as a basis for accurate conclusions, but the much smaller total production on the clipped plot (222 gm) than on the unclipped (500 gm) probably reflects the correct relationship if the plants are clipped close to the ground after panicles have started to develop in a dry season. For clipping under other circumstances the effect might be different. In Nevada, Fleming *et al.* (1942) found that after clipping in 1940, when the plants were at the stage "Seed stalk dough, Leafage green," regrowth was only about 5% of the original production. However, in 1941, when clipped at the same stage, regrowth was slightly in excess of the original growth. There was 4 times as much precipitation in the period of regrowth in 1941 as in 1940, which was believed to

account for the difference in response of the two seasons.

INCIDENCE OF SMUT (*Ustilago bullata*)

The smut of bromegrasses has often been called *Ustilago bromivora* (Tul.) F. von Waldh., but is included in the species *U. bullata* Berk. by Fischer (1937).

B. tectorum and *B. sterilis* were frequently smutted, but the smut was uncommonly observed in the other species of annual bromegrasses. Sometimes so many of the panicles of *B. tectorum* were smutted that shoes were blackened from walking through a stand of the grass, but even in such cases it was always possible to find some normal spikelets. Occasional panicles were observed in which some of the spikelets were smutted and the rest had sound seed, a situation reported also by McAlpine (1910).

Before being planted in the experimental plots, some florets of *B. tectorum* were treated to kill the smut spores which they carried. Two treatments were used: (1) dusting with "Semesan" and (2) soaking in a solution of 1 part commercial formalin and 320 parts water for 5 minutes, followed by rinsing and drying.

The same high incidence of smut was obtained in the early fall plantings of both treated and untreated florets, but in the late fall plantings those from formalin treated florets had about one-half the incidence of smut of the untreated controls. "Semesan" treatment resulted in very little reduction of smut. Even in the controls, however, the incidence was only about one-fifth as high in the late fall plantings as in the early fall plantings. The probable explanation for these results is as follows. By dissemination from surrounding stands of *B. tectorum* the soil had a large supply of smut spores. These smut spores germinated along with the Bromus seeds in the early fall planting and thus infected the seedlings, which is the stage at which infection occurs (McAlpine 1910), even though no spores were carried on the seeds when planted. Because nearly all the smut spores in the soil had germinated and died during the 6 weeks before the late fall planting, infection then resulted from smut spores carried on the seeds. Since formalin killed many or all of these spores, the plants growing from formalin treated seeds had a much lower incidence of smut than the controls in these later plantings.

In the row plots *B. sterilis* had an equal or greater amount of smut than *B. tectorum*, which was about 45% smutted in the early fall plantings. *B. japonicus* had a low incidence, usually much less than 10%. In the remaining species smut was rare.

STAGE WHEN YOUNG SEEDS ATTAIN VIABILITY

How early in development can florets of *B. tectorum* be harvested and contain seeds which will later germinate? To answer this, florets were collected at various stages of development in 1950 and stored in paper sacks in the laboratory. In August 1951 germination tests were made on these samples (Table 12).

TABLE 12. Viability of *Bromus tectorum* seeds collected before maturity at the Lewiston Study Area in 1950. Germination tested (using 100 or more seeds) in August, 1951. Moisture content is percentage of wet weight.

Date collected	Moisture content when collected %	Viability after 1 year %	Stage of plants from which seeds were collected
May 13...	—	90	Mostly green; few of glumes purple and few pedicels with purple joints, remainder green
May 19...	55	93	Fruits half green, half purple; a few with some brown color
May 20...	62	97	Awns often purple, glumes sometimes purple, remainder green
May 27...	62	92	About like previous ones, but slightly more purple
May 27...	55	90	Mostly purple, little green
June 3....	39	100	Plants brown

In the youngest collection viability was high, even though collected at a stage when the fruits had barely started to develop purple coloration, being almost entirely green. The indications are that some viable seeds would result even if panicles were cut before any purple coloration appeared.

In another experiment the *B. tectorum* plants on about 1 sq m were clipped at the ground surface at a time when the plants were entirely green and when the ovaries were in the "dough" stage (May 27, 1950, Lewiston Study Area). It was supposed that no viable seeds would be present, but to be sure, some seeds were removed from the clipped shoots after storage in a paper sack in a laboratory for a little more than one year. The percentage was not determined, but viability was found in some seeds. Perhaps leaving the florets attached to the stems and leaves helped them attain viability, as they may not have become air-dried for a few days after clipping.

It was shown earlier that the dough stage was reached 20 days after anthesis, so there is only a short period after inflorescences appear during which the plants could be mowed without danger of having viable seeds present in the hay.

SEED DISPERSAL

Most florets shattered from the inflorescences within a few weeks after maturity in all the annual bromes studied. In the species of the section Bromium occasional florets were still found in the panicles in the autumn in normal situations, but in *B. tectorum*, *B. sterilis*, and *B. rigidus* (section Eubromus) florets had normally all fallen by that time. Only in a few inflorescences in the lee of large boulders and other such places exceptionally sheltered from the wind were a few florets found attached to the inflorescences of *B. tectorum* in March, 1950.

Attempts were made to study dispersal by dipping the panicles of mature plants, just prior to seed fall, in bright-colored stains so the seeds would be marked as to point of origin. On June 10, 1950, this method was used on plants about 3 dm high. Later in the day, after a strong wind developed, a few seeds were

found up to a meter away from the inflorescences where they were produced. In other trials this method was unsuccessful because the color was not easily detected or because the color faded within a few days.

Dispersal was also studied by use of seed traps of a design adopted after preliminary tests. The traps, 0.25 sq m in area and 6 cm deep, had wooden sides. The bottom was covered by window screen and a layer of muslin, the cloth being necessary as some florets could pass through the screen. The removable top of the trap was covered with 0.5 in. mesh wire cloth. To prevent seeds from being blown out of the trap, a removable piece of 0.25 in. mesh wire cloth was placed about 2 cm above the bottom (Fig. 19). Tests indicated that this construction prevented strong winds from blowing the florets out of the trap.

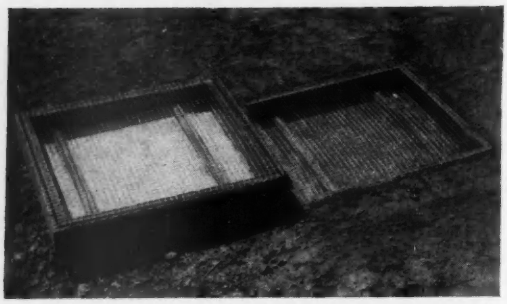

FIG. 19. Traps placed to study dispersal through air compared with that along soil surface of seeds from a stand of *Bromus tectorum* 1 m to the west. Top of left trap 1 dm above soil, that on right flush with soil surface. Catch in 7 weeks was 35 and 143 seeds, respectively. Pullman Study Area, 1951.

Unfortunately the seed traps were not constructed until after seed dispersal had begun. They were placed in the field July 3 and 14, 1951 and left in place until September 1. Counts of seeds caught were made several times during this period (Table 13).

The results are of limited value because much seed had shattered before the traps were placed in the field. However, they support the conclusion obtained by watching florets which were thrown up by hand into the air, that wind ordinarily will not blow them far. It seems probable that all florets caught more than 1 or 2 m away from the source were carried by the small "dust whirls" that frequently develop on clear summer days.

Seeds were blown along a smooth soil surface more frequently than they were carried through the air in the experiment shown in Fig. 19. Two traps were about 1 m easterly (probably the prevailing winds were westerly) from a stand of *B. tectorum*. One trap, 1 dm above the surface, caught 35 seeds; the other, imbedded so the top was flush with the soil surface, caught 143 seeds in seven weeks.

Undoubtedly wind and possibly water are important for movement for short distances such as 1 m. For longer distances, dispersal by animals is much more likely to be important. The barbed florets of the species in the section Eubromus are ideally adapted to being picked up by clothing and fur, as sheep men testify. The species in the section Bromium, however, are not sharp or barbed and are less readily picked up in this way.

TABLE 13. Numbers of *Bromus tectorum* seeds caught in traps from July 13 to September 1, 1951. Unless otherwise indicated the tops of traps were 1 dm above the soil surface.

Location	Horizontal distance from stand of *Bromus tectorum* in m	Number of seeds caught
Forest Nursery, State College of Washington, Pullman. Field of grass with some *B. tectorum* at indicated distances to west	1	15
	3	0
	5	0
	10	4
	15	0
	25	1
Same, except at indicated distances to north of a stand of *B. tectorum* (about 40 m from a stand to the west)	2	0
	5	0
	10	0
	15	0
	25	0
On fence post 165 cm high, beside stand of *B. tectorum* to west (windward)	0	1
Near Lewiston Study Area, in edge of wheat stubble. Stand of *B. tectorum* at indicated distances to northwest	1	4
	2	0
	5	1
	10	0
	15	1
	20	1
On posts surrounded by *B. tectorum* at the Lewiston Study Area		
Ht. above ground		
52 cm	0	1
75 cm	0	0
146 cm	0	0
147 cm	0	0

GERMINATION

Germination of seeds of *B. tectorum*, *B. japonicus*, *B.brizaeformis*, *B. rigidus*, and *B. commutatus* was studied. Primary attention was given to the relationships of age, temperature and light to the germination of *B. tectorum*.

Unless otherwise indicated, all germination tests were made using petri dishes (diam 9 cm, depth 1-1.5 cm) containing moist filter paper. Before use the petri dishes were carefully washed, rinsed in tap water and then rinsed twice in distilled water. After testing a few kinds of filter paper, Whatman No.2 was adopted, as no indication of detrimental effects was found, and it possessed good water holding properties. Two sheets per dish were usually used. Enough distilled water was added every one or two days to maintain a small meniscus between the seed and the filter paper.

To ascertain if the amount of water used was optimal, a series of tests was made using measured amounts of water. The results (Fig. 20) indicate only minor differences in the rate of germination, yet

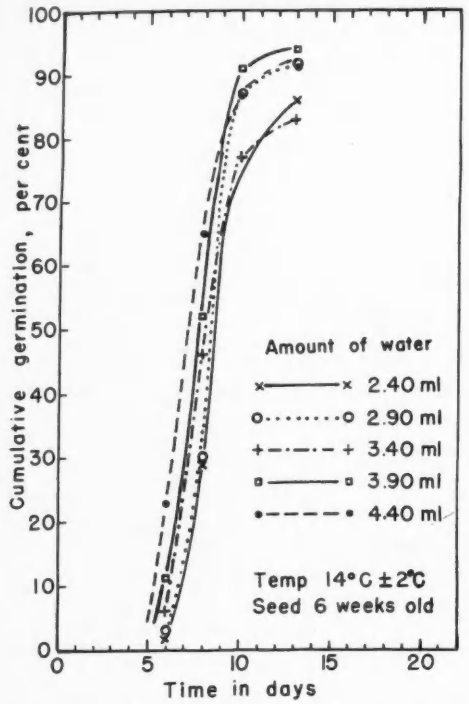

FIG. 20. Effect of different amounts of water on germination of *Bromus tectorum* seeds on filter paper in petri dishes.

the range in wetness was greater than normally occurring in the other tests. Hence it appears that variation due to the degree of wetness of the filter paper was negligible.

Seedlings were counted as having germinated when (1) both a plumule and a radicle had developed and (2) when the plumule had attained a length of 1 cm. Germinated seedlings were removed as they were counted. These standards indicate slower germination than that found by those workers who count a seed as germinated when the plumule appears. In favorable conditions the radicle was plainly visible in 24 hours, and the plumule in 48 hours. This criterion of 1 cm for plumule length was longer than necessary for satisfactory results, but assured sufficient time to observe for abnormal development of the seedling. For example, after nitric acid treatment was applied to some seeds a visible plumule about 1 mm long was produced at about the usual rate, but the embryos died at that stage of development.

The 1950 seed collections were threshed and cleaned in equipment specially designed for small samples of grains. The equipment appeared to do a good job, but in subsequent germination tests it was found that the embryo had been injured in one-third to one-half of the seeds by the threshing operation. Thereafter all threshing was done by hand and a wind-type seed cleaner used to separate the seed from chaff. In nearly all cases 100 seeds per test were used. Since the purpose of the germination tests was not to ascertain the percentage of viable seeds but to learn the effect of various environmental conditions on germination, only those seeds were used which appeared well developed.

To study the effects of age, light and temperature on germination of *B. tectorum*, a series of tests was conducted in both the light and dark at 10, 15, 20, 25 and 30°C (accuracy ± 1°) on the same seed lot when newly ripened, when 4 weeks old, and when 7 weeks old. These tests were also made twice on seed one year old, so that the effect of light and dark at these 5 different temperatures was obtained on seed of 4 different ages (Fig. 21).

The maximum temperature for germination was 15°C for new seed, but increased with age so that one seedling (abnormal) was produced at 35° in a test of 5-months-old seeds. Likewise the optimum temperature for germination increased with age as follows: (1) 10° for new seeds (2) 15° for 4-weeks-old seeds (3) 15 to 20° for 7-weeks-old seeds, and (4) 20° for 1-year-old seeds. Complete germination was obtained for the seed 4 weeks old and older, but only about half of the new seed germinated at the best temperature tried. Germination of year-old seed was tested in the dark at 5°C. By 24 days 16% had germinated, and by 34 days 96% had germinated. Using 1-month-old seed germination was only 75% in the same time. At this, as at the other low temperatures, the quality of seedlings produced was excellent.

In 1947 the writer found that light had a definite retarding action on germination of 5.5-months-old seeds of *B. tectorum* (Fig. 22). The petri dishes of seeds were so placed on a greenhouse bench in Missoula, Montana during November and December that they were exposed to skylight but shaded from direct radiation from the sun. Intensities of 50 and 10% of full diffuse daylight were obtained by placing appropriate gratings several centimeters above the dishes. Those in the dark were enclosed in lightproof cardboard boxes and left beside the others. Direct sunlight was excluded in order to avoid important temperature differences among the treatments. Accurate temperature records were kept of the air beside the petri dishes in both the light and dark using calibrated maximum and minimum thermometers as well as ordinary laboratory thermometers. Temperature differences were found to remain less than 1°C. Since air temperatures outside the dishes might differ from that inside the dishes, a series of trials were made to check this factor. In diffuse daylight in a greenhouse at midday the air inside the petri dishes was found to be 0.6°C warmer than outside. About 40 cm below a reflector containing two 40-watt fluorescent tubes the temperature difference was 0.4°C. The air temperature differences between treatments were thus shown to be no greater than 1.5°C and usually less. From the studies of the effect of temperature on germination (Fig. 21) it seems justified to assume that the differences in germi-

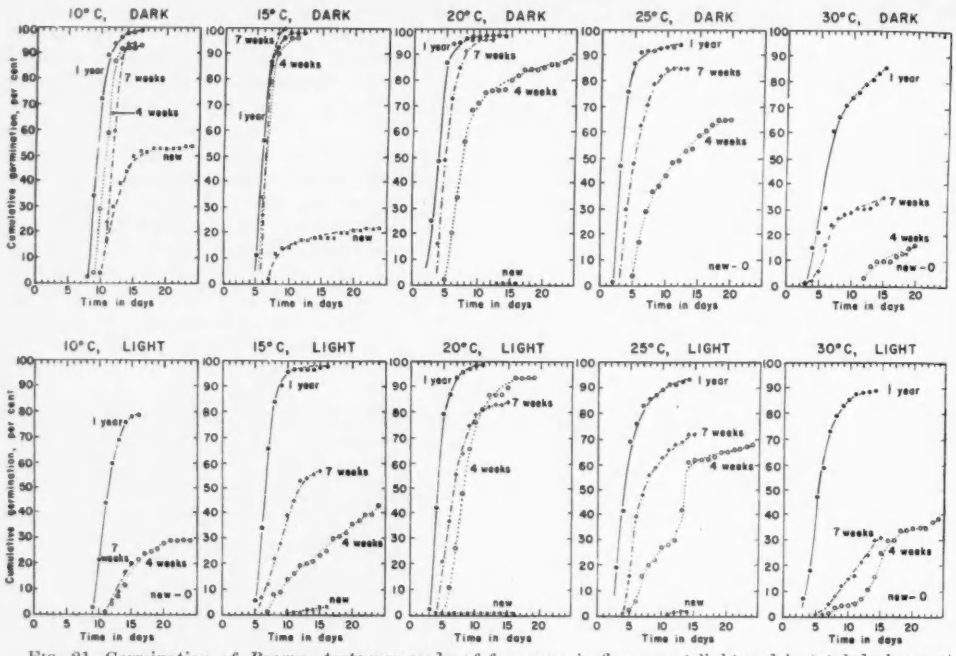

FIG. 21. Germination of *Bromus tectorum* seeds of four ages in fluorescent light and in total darkness at 10, 15, 20, 25, and 30°C (100 seeds per test).

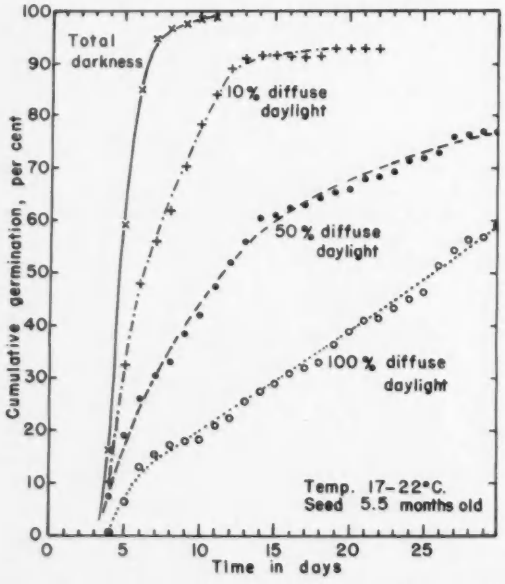

FIG. 22. Effect of diffuse daylight on germination of *Bromus tectorum* seeds in a greenhouse in Missoula, Montana, Nov. 28 to Dec. 27, 1947.

nation in the light and dark are due primarily to effects of radiation apart from temperature.

To study the effect of light at controlled temperatures it was necessary to use fluorescent light instead of diffuse daylight. Special boxes with glass tops were placed in a cold room at 5°C and maintained at the desired temperatures of 10, 15, 20, 25 and 30°C by use of thermostatically controlled heaters. Two 40-watt fluorescent tubes, one white and one soft white, in a standard fixture were suspended over these boxes so that a light intensity of 9 to 18 luxes (100 to 200 fc), measured with a Weston Illumination Meter Model 603, was present at the level of the petri dishes in the boxes.

The results (Fig. 21, 23) indicate that the response to light is complex. It was found that (1) the effect of light decreased with increasing age of the seed, (2) the effect of light is least at the most favorable temperature and greater at less favorable temperatures, (3) at low temperatures light is either inhibiting or retarding for young seed, (4) at unfavorably high temperatures light becomes somewhat stimulating. In such cases, however, seedlings are less vigorous than at lower temperatures, and may develop abnormally. It should be noted that this stimulation is based only on tests in fluorescent light. The available evidence indicates that daylight has a stronger retarding effect than did the fluorescent light, and perhaps no stimulation would result with daylight at high temperatures.

Germination tests were made on seed 7.5 years and 5.5 months old in diffuse daylight and in the dark in a greenhouse in winter (temperature range 19 to 26°C). The old seed germinated equally in the light and dark, but the 5.5-month-old seed germinated

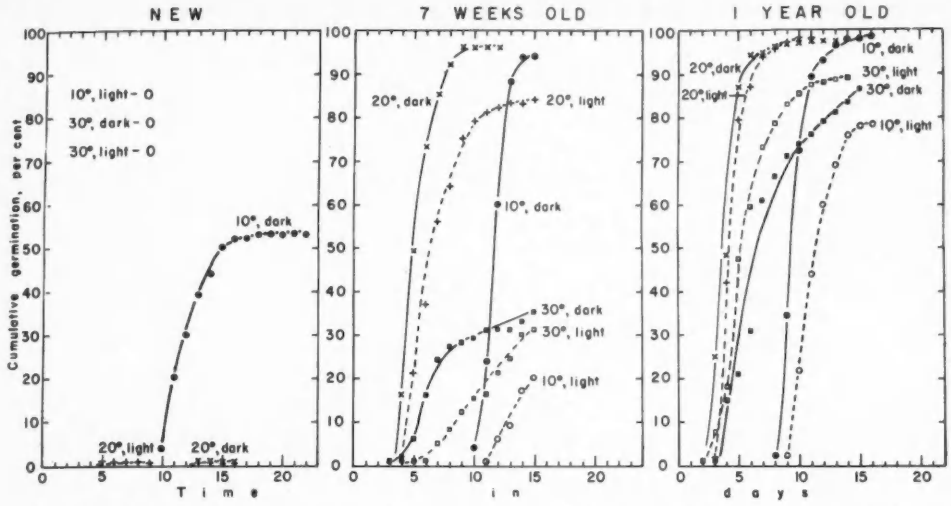

FIG. 23. Effect of age on germination of *Bromus tectorum* in fluorescent light and in the dark at 10, 20 and 30°C. (This is a different arrangement of some of the data shown in figure 21.)

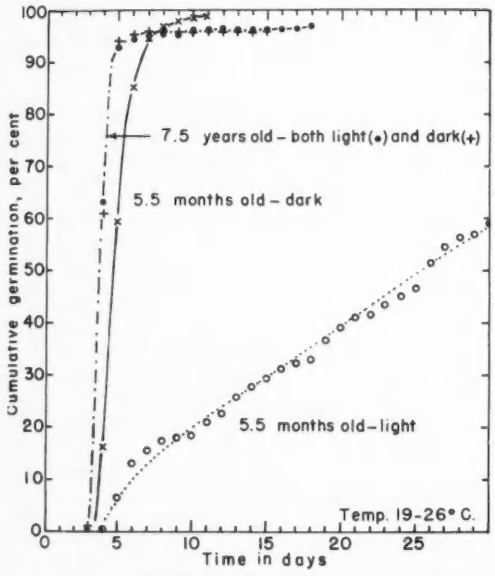

FIG. 24. Comparison of germination of 5.5-months and 7.5-year-old seeds of *Bromus tectorum* in the dark and in diffuse daylight in a greenhouse.

less well in the light (Fig. 24). The absence of an effect of light on germination of old seed was confirmed on two other samples, 6.5 and 7.5 years old. These seed samples, collected locally, had been stored in paper sacks in a laboratory at Missoula, Montana.

In most tests made in the dark the seeds were exposed to light while counting the number germinated each day. To ascertain if this short exposure had any noticeable effect, a dish of dry seeds was wet in total darkness, then wrapped in a black paper and placed in a 3-piece photographic film box. The box, kept at 15°C, was opened in 9 days, at which time 99% had germinated and were in good condition, showing that light is unnecessary for germination.

Seeds of *B. tectorum* in a series of petri dish tests were exposed to different daily photoperiods ranging from 0 to 24 hours. They were kept at 10°C in a constant temperature cabinet and illuminated with white fluorescent light at an intensity of about 18.5

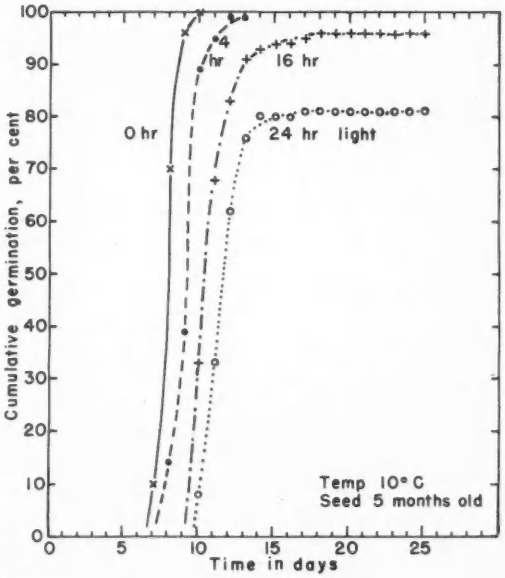

FIG. 25. Effect of length of the daily photoperiod of fluorescent light at an intensity of 18.6 luxes on germination of seed of *Bromus tectorum*.

luxes (200 fc). The results indicate that the effect of light in retarding germination is somewhat proportional to the length of daily exposure to light (Fig. 25).

Partly because germination was excellent at constant temperatures, only some preliminary trials were made using alternating temperatures. Combinations of 7° and 25°, and 14° and 25°C, resulted in faster germination than at either temperature if constant, but the combination of 7° and 14° resulted in germination intermediate between the rate at constant 7° and constant 14° (Fig. 26). The explanation seems to be that alternation is of no benefit if confined to a range in which constant temperatures result in good germination, but alternation seems to reduce or eliminate the detrimental effect of some temperatures which are unfavorable if constant.

To determine the effects of various depths of planting on emergence, a series of trials was made in the greenhouse at Pullman, Washington in the winter of 1950-51. Seed was planted on the surface and at depths of 1, 2, 4, and 6 cm in loam from the Lewiston Study Area. Each flat was watered and checked daily. To eliminate drought and light factors from the flat which had seeds on the soil surface, a cover was placed over this flat. The results show that from the surface to a depth of 2 cm all seedlings emerged (Fig. 27). A depth of 4 cm apparently caused elimination of some seedlings, probably the weaker ones. Only a few, which appeared weak, emerged from a depth of 6 cm.

Five-months-old seeds of *B. tectorum* floating on water and submerged in water were placed both in the dark and in diffuse daylight in the greenhouse at Pullman, Washington on December 20, 1950. Dis-

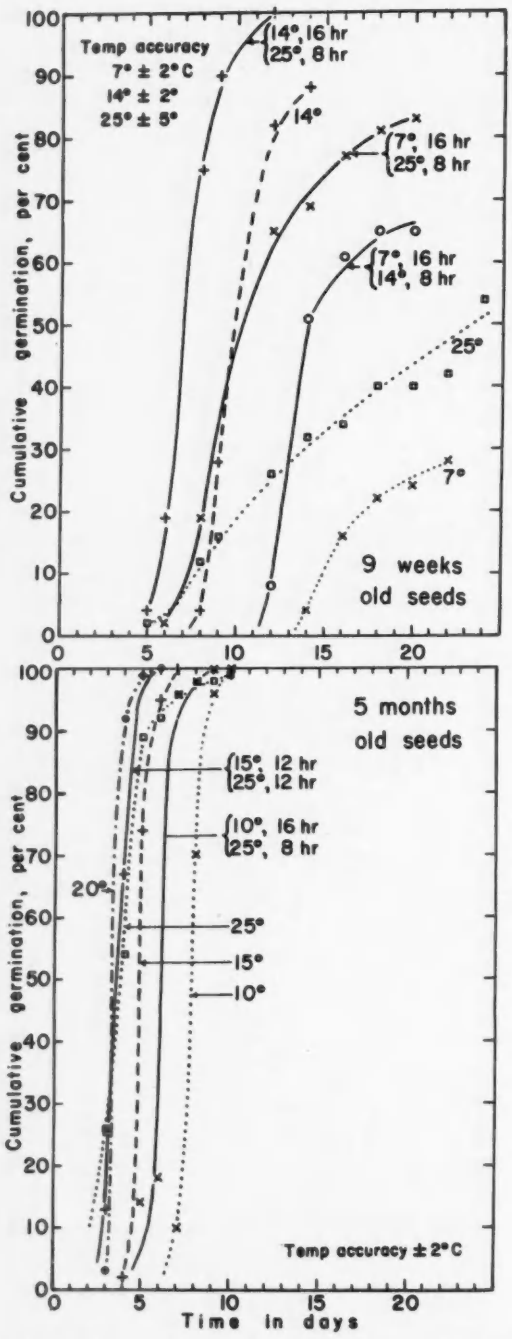

FIG. 26. Comparison of the effects of constant and alternating temperatures on germination of *Bromus tectorum* seeds in the dark.

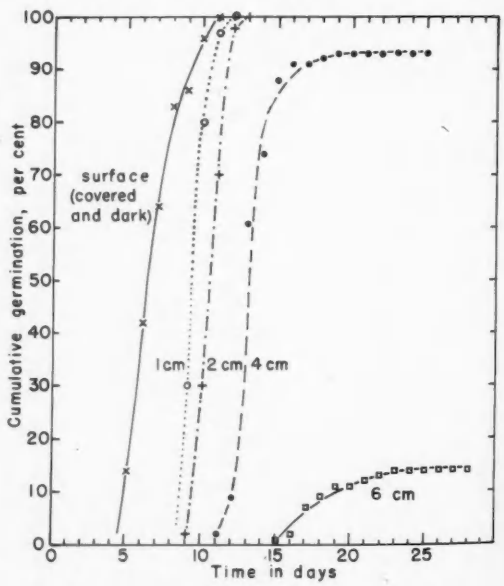

FIG. 27. Effect of depth of *Bromus tectorum* seed in loam soil on emergence of the plumule. Greenhouse tests in winter using soil from Lewiston Study Area, watered once daily.

turbance of the water had to be avoided to prevent the seed from sinking. Germination was as rapid in floating seeds as in those in petri dishes, but submerged seeds germinated less rapidly and became infected by fungi in a week or more (Fig. 28). As on moist filter paper, diffuse daylight was found to retard germination. In a similar trial of seeds floating on and submerged in water made using white fluorescent light at 9 to 18 luxes instead of daylight the results were in agreement with the previous trial.

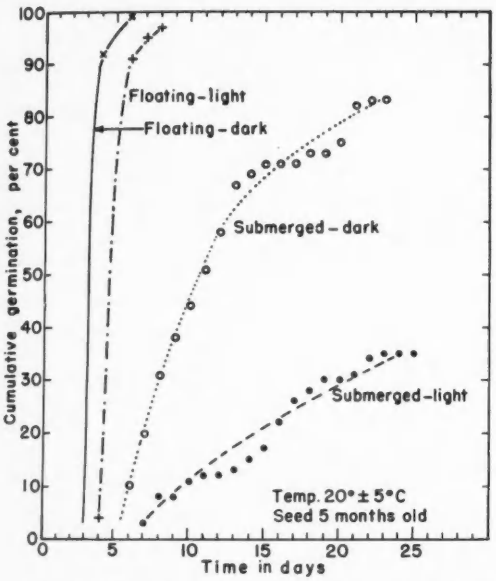

FIG. 28. Germination of *Bromus tectorum* seeds floating on and submerged in water in diffuse daylight and in the dark.

No difficulties arose due to growth of fungi in any of the many germination tests on these annual bromes. Fungi did not develop during the first two or more weeks of germination and the fungal growth remained localized, never filling the petri dish as sometimes occurred with other seeds.

Because fungi which develop on seeds are often carried with the seed from its place of collection, W. Bridge Cooke identified the fungi which had developed on some of the Bromus florets ("seeds") remaining in the petri dishes 3 to 6 weeks after the start of germination tests. The fungi were identified as follows: *Acremoniella verrucosa* Togn., *Alternaria tenuis* Nees (group), *Aspergillus unguis* (Emile-Weil & Gaud.) Th. & Rap., *Cladosporium herbarum* (Pers.) Link, *Helminthosporium cyclops* Dreschl., *Hormodendrum cladosporioides* (Fres.) Sacc., *H. viride* (Fres.) Sacc., *Penicillium expansum* Link, *Stachybotrys atra* Corda, and *Stemphyllium consortiale* (Thüm.) Groves & Skolko. A report has been published indicating on which Bromus species each of these fungi occurred (Cooke & Shaw 1952). Perhaps if Bromus seeds are in moist but otherwise unfavorable conditions for germination for a number of days, these same fungi would attack the seeds in natural conditions as they did in the petri dishes.

A preliminary check was made to find if there was any difference in germination between the lowest floret and the uppermost fertile floret in a spikelet. Often two florets were filled, occasionally more, and in depauperate specimens only one. In two different collections 50 of the uppermost fertile florets and 50 of the lowest florets were removed from spikelets and subjected to germination conditions. The seeds of the two collections, 1- and 4-weeks old when the tests were started, were subjected to a temperature of 14°C in the dark. Germination was good, occurring in 7 to 15 days. In the tests from both collections the upper florets germinated more rapidly than the lowest florets, the difference in time at equal percentages generally amounting to one day. No such tests were conducted on old seed, but it seems likely that this difference would disappear with aging. Inasmuch as the lowest florets were slightly earlier in development than the upper florets during the time of flowering and fruit development, this difference cannot be attributed to earlier maturity of the upper florets.

The effect of age, temperature and fluorescent light on germination were studied in *B. brizaeformis, B. commutatus, B. japonicus,* and *B. rigidus,* but a lesser number of ages were tested than for *B. tectorum* and no tests were run in diffuse daylight.

New, 4-weeks-old, and 1-year-old seeds of *B. japonicus* were tested in fluorescent light and in darkness at 5 different temperatures (Fig. 29). The optimum and maximum temperatures for germination increased with age, and fluorescent light was inhibiting for new and retarding for older seed at favorable temperatures. For 4-weeks-old seed, light was somewhat stimulating from 20 to 30°C, but in 1-year-old seed those in the dark germinated better than those in the light at all temperatures tested. These results for *B. japonicus* are similar to those for *B. tectorum.*

In general *B. brizaeformis* (Fig. 30), *B. commutatus,* and *B. rigidus* showed similar germination responses to temperature and fluorescent light in relation to age as did *B. japonicus* and *B. tectorum,* but differences were found in the rate of germination at various temperatures. For example, partial germination occurred in new seed of *B. brizaeformis* at 20°C and in new seed of *B. rigidus* at 25°C, whereas new seed of *B. tectorum* and *B. japonicus* did not germinate at all at 20°C or above. For 1-year-old seeds the number of days' time to reach 50% germination was found to be:

	10°C	20°C	30°C
B. tectorum	9.25	3.0	7.0
B. rigidus	10.25	3.25	3.5
B. brizaeformis	10.5	4.75	4.0
B. japonicus	12.5	5.75	6.0
B. commutatus	14.5	6.75	5.5

These data indicate that *B. tectorum* is the fastest to germinate at low temperatures, but the slowest at

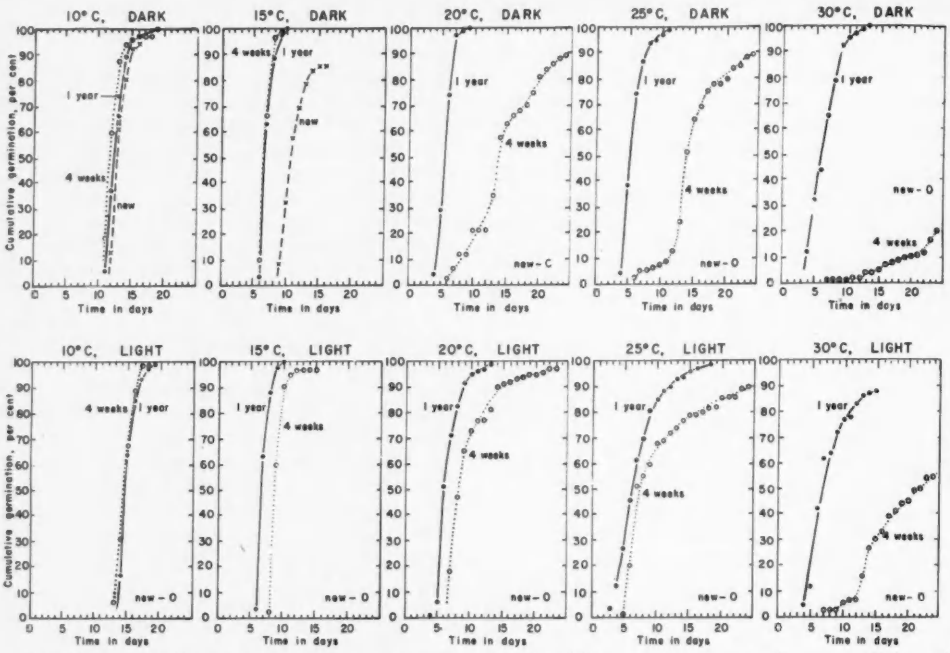

FIG. 29. Germination of new, 4-weeks, and 1-year-old seeds of *Bromus japonicus* in fluorescent light and dark at 10, 15, 20, 25, and 30°C. (100 seeds per test.)

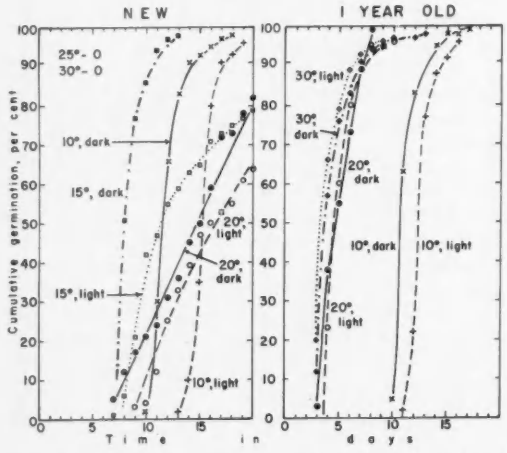

FIG. 30. Germination of new and 1-year-old seeds of *Bromus brizaeformis* in fluorescent light and dark at 10, 15, 20, 25, and 30°C. (100 seeds per test.)

high temperatures of these 5 species, that *B. rigidus* is the fastest to germinate at high temperatures and that *B. commutatus* is the slowest at low temperatures. Only tests run on various collections of each of these species would show if these comparisons are valid for all populations of each species.

The germination characteristics reported for these species are sufficient to explain why their seeds, which commonly ripen in May and June, germinate readily during the autumn rainy periods but rarely develop, at least in *B. tectorum*, following summer rains. Young seed will not germinate above 20 to 25°C, but soil surface temperatures regularly exceed this in the summer. By fall, the temperature of the soil surface is lower and the seeds will then germinate at temperatures as high as 30°C. In addition the retarding influence of light decreases as the seeds age, and by autumn they will have had a greater chance to work into the litter or soil crevices where light intensity will be less. Thus the internal changes in response are correlated with seasonal changes in the environment to fit these species to their role as winter annuals. If unusually cool wet weather lasts for several days, these species could be expected to germinate in July or August.

The effects demonstrated here of light and temperature on germination in the annual bromes are in agreement with results reported on certain other plants. Gordon (1951) reported a decrease in sensitivity of *Phleum pratense* seeds to temperature and light with increasing age. Spalding (1909, p. 71) observed that summer temperatures prevented germination of seeds of winter annuals. Went (1948) experimentally ascertained that temperature was a controlling factor in determining whether summer or winter annuals germinated in desert soil.

SEED LONGEVITY IN THE FIELD

Do all seeds of *B. tectorum* germinate the first fall or winter after they are produced, or do some remain viable for more than one year in the field? To check

on this, enclosures consisting of frames about 0.9 m square covered by window screen on the sides and top were constructed on May 27, 1950 at the Lewiston Study Area and on June 8 at the Pullman Study Area. After clipping all plants inside the enclosures as close to the ground as possible, a piece of muslin cloth was placed on the soil surface to catch any florets of Bromus which might pass through the screen. By cutting and removing all plants in the spring it was thought that if any developed later it would prove that they had arisen from seed which had remained viable but ungerminated in the soil. One difficulty arose, unfortunately. The plants were clipped after inflorescences had developed, but while they were yet entirely green. At the time of clipping it was believed that no viable seed had been produced, but on testing the tops after storage for one year in paper sacks, it was found that some viable seeds were actually present. During clipping a few florets might have broken off and remained in the enclosures, so the origin of any plants developing later could not be known. In the enclosure at the Pullman Study Area no *B. tectorum* plants were found a year later, but 3 were present in the enclosure at the Lewiston Study Area. The small number seems to justify the conclusion that even if seeds of *B. tectorum* did remain ungerminated yet viable for a year it was an uncommon occurrence. This conclusion was supported by numerous observations of small plots at the time germination and seedling establishment were taking place. Such observations gave the strong impression that all seeds germinated as soon as external conditions were favorable.

To study the effect of burial on seed viability and germination, seeds of *B. tectorum* collected locally were buried about 11 cm and 23 cm deep in a loam in the Bitterroot Valley east of Florence, Ravalli County, Montana on September 21, 1947. Three replications were installed. For recovering the seeds later, glass cloth sacks were used. Some seeds were enclosed in the sacks and some were placed beside them in the soil. Another test was installed a few miles southwest of Missoula in similar soil on October 24, 1947. All four tests of buried seed were dug up on March 27, 1948. In all cases all viable seed had germinated in the soil. Those buried September 21 were found to be dead, but those buried October 24 were still alive and continued growth when placed in a moist chamber.

To check the effect of deeper burial and burial in heavy soil, two sets of duplicated tests were installed on October 15, 1950. One was in loam soil at the Lewiston Study Area, the other in silty clay loam at the Pullman Study Area. A pair of holes were drilled close together with an orchard soil auger. In one hole seeds in glass cloth sacks were placed at 10, 25, 50, and 100 cm depths. In the other hole seeds not enclosed in a sack were placed at the same depths. The soil removed while making the holes was saved in cans and replaced in the order in which it occurred in the profile. The soil was tamped in place as uniformly as possible so as to occupy the original volume.

These buried seeds were removed from the soil in August, 1951. All appeared to have germinated, many dead roots and plumules being matted together. The seeds had become blackened by microbial action. In the laboratory these matted samples were placed in petri dishes on moist filter paper to find out if any viable seeds remained. Surprisingly, germination occurred in some seeds in 7 of the 24 samples (Table 14). The explanation for this is unknown. Since the number of viable seeds does not consistently increase with depth, the absence of sufficient aeration does not seem to be a satisfactory hypothesis. Moisture content was ample for germination for a number of weeks at all depths. Germination inhibitors have been found in some seeds (Evanari 1949). Perhaps seeds of *B. tectorum* possess enough of such a substance so that when large numbers of seeds are together as in these tests (300 to 500 per sample) germination is hindered.

TABLE 14. Viability of *Bromus tectorum* seeds after burial at four depths from October 15, 1950 to July, 1951. The 300-500 seeds per test had germinated in soil and dead shoots and roots formed matted mass on exhuming. Viability tested by placing portion of sample in petri dishes.

Location	Percentage Viable			
	10 cm	25 cm	50 cm	100 cm
Lewiston Study Area				
Free in soil				
Test No. 1	0.03	0	0	0
Test No. 2	4	0	0	0
Pullman Study Area				
In glass cloth sack				
Test No. 1	0	0	0	0
Test No. 2	0	3	5	0
Free in soil				
Test No. 1	0	5	0	18
Test No. 2	0	5	0	0

It was noticed that some seedlings developing in the petri dishes were from seeds that had a dead radicle attached. To test the possibility of this occurring, seedlings of *B. tectorum* at various stages of development were air-dried for 19 days and then rewetted. Viability was found to be present in seedlings which had produced radicles up to 15 mm long if the plumule was still so small as to be invisible or barely visible without magnification when air dried. Although this indicates that the seeds found viable after burial for 10 months might have previously germinated and still be viable, it does not explain why some developed beyond the point at which they can survive desiccation and others did not.

Seed Longevity in Storage

Samples of *B. tectorum* seed 5.5, 7.5, 10.5 and 11.5 years old, collected in western Montana by Joseph Kramer and stored in paper sacks in a laboratory at Montana State University, Missoula, gave 95 to 100%

germination in petri-dish tests. Since these were the oldest samples available, the length of time that seeds can remain viable was not ascertained.

DISCUSSION

Discussion has been included throughout the paper in connection with each topic, so it remains only to include some interrelationships not previously mentioned.

Apparently *Bromus tectorum* became established in both the eastern and western parts of the country between 1860 and 1900 (Bennett 1888, Britton 1889, Robbins 1940, and Warg 1938). Although it constitutes only a minor part of the vegetation in humid areas, it has become a conspicuous and often a dominant part of the vegetation in semi-arid regions since its introduction. Its striking success in such places is partly explained by some of the findings of this study.

Germination at the most favorable season is highly favored by a mechanism involving changing reactions with age to light and temperature. Seeds do not germinate in the summer following occasional rains because for the first several weeks following maturity they require low temperatures. For example, no new seeds would germinate if the temperature was above 15°C, and in 4-weeks-old seeds only partial germination occurred above 15°C. Day temperatures of the soil surface regularly are in the 30's and 40's in the areas where *B. tectorum* is common, distinctly above the maximum for germination. Reinforcing this temperature effect is a retardation of germination by light in seeds only a few weeks old. By autumn, when soil moisture is apt to be dependable for establishment of the seedlings, both the external and internal conditions are more favorable for germination. Days are shorter and cooler, and the seeds will germinate at temperatures as high as 30°C. Thus when autumn rains come, germination is generally rapid and complete. At 20°C all seeds in the autumn produce plumules 1 cm long in 5-6 days, and at 10°C in 8-10 days. Germination is much slower at 5°C, taking 25-35 days, but normal vigorous seedlings are produced even at that temperature. In keeping with this ability to germinate at low temperatures, all North American collections of *B. tectorum* were winter hardy at Lewiston, Idaho and Pullman, Washington, and grew noticeably during the winter at Lewiston where the winters are mild.

Further helping to explain its success in areas of summer drought are its rapid maturity in the spring and its rapid development of a deep root system. In this study roots were found to be densest in the upper 3 dm, but roots of unfertilized plants extended more than 1.5 m deep in a loam near Lewiston, Idaho. That these deeper roots are important to the plants was indicated by the continued growth of the tops after all available water was gone from the upper 6 dm of soil. This deep root system, coupled with the rapidity of germination and seedling development, helps account for the strong competition given to the young plants of perennial grasses.

The great increase in growth resulting from nitrogen fertilization seems to have been due in part to (1) utilization of a greater amount of water in the deeper soil layers as a result of a more extensive root system than in the unfertilized plants, and (2) the production of more dry matter per gram of water used by the nitrogen fertilized plants than by unfertilized plants. This indicates, at least for annuals, that water is not the only limiting factor in semi-arid climates, and that altering other conditions can affect both the degree of utilization and the efficiency of use of the available water.

Any annual must be a good seed producer even in unfavorable conditions, and *B. tectorum* is well fitted in this characteristic. Even tiny plants 4-5 cm high, so small they are easily overlooked, produce one culm bearing one seed. There is a great difference between such a plant and one a meter tall with many culms producing hundreds of seeds, such as occur in fertile soils with favorable moisture conditions if competition is light.

The difficulty of eliminating *B. tectorum* by mowing is shown by the following observations. The plants were generally killed by mowing if they were cut near the ground as soon as purple coloration began to develop in the inflorescences. By this time, however, seeds were sufficiently developed so that they would later germinate. Thus, if any culms were left, or even if some florets were broken off and remained on the area, as is likely to happen, new plants could later develop. However, if mowing is done before viable seed can result, the plants will probably regenerate new culms, judging by the results of this study. Mowing does reduce the number of seeds per unit area (Friedrich 1945) but it is clear that no stage can be found which will assure complete kill or absence of seeds. Also, it was shown that *B. tectorum* must be cut well before the dough stage is reached if one wishes to be sure that the hay will contain no viable seed.

The studies of phenology, winterhardiness, cold requirements and root development help explain the differences in distribution of some of the annual bromegrasses. For example, the lack of winter hardiness of *B. rubens* and *B. rigidus* seems reason enough to account for their absence from all but the supposedly warmest areas of the Columbia Basin.

According to H. H. Hopkins (personal communication), *B. tectorum* has decreased and *B. japonicus* has increased in recent years around Hays, Kansas. Perhaps the tendency for a greater portion of the annual precipitation to come in the summer in Kansas than in the Great Basin, where *B. tectorum* is abundant, tends to favor *B. japonicus* because of its later time of maturity (3 weeks later in row plots at the Lewiston Study Area) and more extensive root system. Supposedly these factors would increase seed yield. Studies are needed to confirm or disprove this hypothesis, such as studying relative seed production of the two species in the Great Basin and in the Great Plains.

Less study was given to other annual bromes than

to *B. tectorum*, but some differences were noted among the species in phenology, winter hardiness, root development, and germination response to temperature. Much more study is needed to explain why the species vary in their habitat preferences, but the differences in response give indications of the causes for these variations. For example, the restriction of *B. rubens* and *B. rigidus* to areas of lowest elevation in the Columbia Basin seems to be correlated with the fact that they are less winter hardy than the other species. Also, it seems likely that the earlier maturity of *B. tectorum* than of *B. commutatus*, *B. japonicus*, and *B. brizaeformis* helps explain why it occurs in drier locations than the latter three species, but certainly other factors are important in this difference.

SUMMARY

Ecological studies were conducted primarily on *Bromus tectorum* and secondarily on 9 other species of annual bromes (*B. brizaeformis*, *B. commutatus*, *B. japonicus*, *B. mollis*, *B. racemosus*, *B. rigidus*, *B. rubens*, *B. secalinus*, and *B. sterilis*), all 10 of which have been introduced from Eurasia into western United States. Experimental studies were carried on near Lewiston, Idaho and at Pullman, Washington. Many field observations were made in Washington, Oregon, Idaho and Montana.

1. *Genetic variation.* The genetic variability of *Bromus tectorum* was studied in plantings of 24 collections of seed from various geographic locations. Differences observed were: (1) all North American collections were winter hardy, but that from Jerusalem, Israel winterkilled about 95%, (2) time of maturity varied about 3 weeks, (3) size variations were found, the taller strains in the North American collections averaging 25% higher than the shorter strains, (4) pubescence on the lemmas varied continuously from scaberulent to thickly pubescent.

2. *Habitats.* The habitats are described where annual bromes occur in the region studied. Quantitative data show that some of these bromes occur as minor constituents of little disturbed native grasslands.

3. *Phenology of species.* Time of maturity varied about three weeks among the various species. The order of maturity was approximately as follows: *B. sterilis*, *B. tectorum*, *B. racemosus*, *B. mollis*, *B. commutatus*, *B. secalinus*, *B. brizaeformis*, and *B. japonicus*. Because of winter injury, accurate comparisons were not possible for *B. rubens* and *B. rigidus*, but probably the former matures about the same time as *B. tectorum* and the latter a bit later.

4. *Winter injury.* All fall-seeded plants of *B. rubens* except one individual winterkilled in the study areas. In *B. rigidus* much injury occurred, resulting in 100% mortality at Pullman and roughly 75% mortality at Lewiston. All other species were winterhardy at Lewiston, Idaho. At Minneapolis, Minnesota, both *B. rubens* and *B. rigidus* were completely killed, and several species were injured considerably. *B. tectorum* showed no winter injury.

5. *Roots.* Roots of *B. tectorum* in natural stands were found to extend into the caliche layer whose upper limit was 1.2 to 1.5 m below the surface of the loam soil at the Lewiston Study Area. Results of the lithium chloride tracer technique indicate that roots extended to a depth of 2 m, 0.5 m into the caliche layer. Root weight determinations in row plots at the Lewiston Study Area showed that *B. japonicus* and *B. commutatus* produced over twice as much root weight per unit area of soil surface as did *B. tectorum*, but root weights of *B. sterilis*, *B. brizaeformis*, and *B. racemosus* were only 45 to 70% of that of *B. tectorum*.

6. *Effect of nitrogen fertilizer.* Ammonium nitrate fertilizer added to natural stands of *B. tectorum* at rates equal to 7.2 gm of nitrogen per sq m (80 lbs/A) more than doubled root growth and trebled height growth, shoot weight, and seed production per unit area. Even though they were larger, fertilized plants remained greener during a six weeks' drought in March and April than did unfertilized plants, presumably due to the greater ability to obtain water in the deeper layers of soil as a result of the increased root growth.

7. *Soil moisture.* Soils at both study areas were wet at least 4 ft deep by precipitation in the fall, winter and early spring. At the Lewiston Study Area *B. tectorum* reduced the soil moisture to permanent wilting to a depth of 7 dm in natural stands and to a depth of 11 to 13 dm in nitrogen fertilized natural stands. Soil moisture was depleted to permanent wilting to about the same depth in the sparsest plantings (0.5-1 plant per sq dm) as in the densest plantings (20-30 per sq dm) when the plants were mature.

8. *Flower initiation.* Of the 10 species only *B. rubens* flowered normally when spring planted, even when a sufficient moisture supply was available. The other nine species must be subjected to cold temperatures if flowering is to be normal.

9. *Anthesis.* In one inflorescence of *B. tectorum*, dehiscence of anthers in different florets occurred over a span of 11 days, starting in some upper spikelets before all of the panicle had emerged from the sheath. Within a spikelet pollen was shed earlier in the lowest floret than in upper florets.

10. *Effect of clipping.* Clipping of plants at a height of 1 cm prior to emergence of the inflorescences reduced the subsequent yield only slightly. Progressively later clipping caused progressively greater reduction in yield. When the dough stage was reached and purple coloration was just starting clipping caused death of the plants.

11. *Smut.* The incidence of smut (*Ustilago bullata*) was much lower in late fall plantings than in early fall plantings unless the smut spores were present on the seeds, perhaps because smut spores in the soil had germinated and died before the late fall planting date.

12. *Shoot and seed production.* In early and late fall plantings at four densities ranging from 0.5 to 40 plants per sq dm the shoot and seed production was similar at all densities but some reduction occurred at the highest densities. Under the conditions

tested the production at average densities was 5-6 gm of oven-dry tops and 400 seeds per sq dm.

13. *Dissemination by wind.* The little information gathered on dispersal indicated that florets ("seeds") of *B. tectorum* are carried a few meters or less by straight wind. "Dust whirls" probably carry seeds much further.

14. *Germination.* Differences among the species were found in the rate of germination at different temperatures, ranging from 3 to 7 days at 20°C. The optimum and the maximum temperatures increased with increasing age of the seeds for the first several months. Diffuse daylight caused a strong retardation in germination of *B. tectorum* seeds 5.5-months-old at favorable temperatures, but had no effect on seed 6.5 and 7.5-years old. White fluorescent light at 9-18 luxes (100-200 fc) caused some retardation at low temperatures and some stimulation at unfavorably high temperatures, but there is some doubt as to whether daylight would give the same stimulation as did the fluorescent light.

15. *Longevity of seeds in the field.* Observation and experiments indicate that probably all or nearly all seeds of *B. tectorum* germinate the first season that external conditions are favorable.

16. *Effect of depth on emergence.* Emergence of all plumules resulted from burial of florets ("seeds") of *B. tectorum* at a depth of 2 cm in a moist loam in the greenhouse. At a depth of 4 cm, 93% emerged, but at 6 cm only 14% emerged.

17. *Effect of burial on seeds.* Most florets buried in the early fall at depths of 11, 25, 50, and 100 cm germinated and died but in a few cases some viable seeds were still present the next summer. The reason for the occasional viable seed is not known.

18. *Effect of desiccation on seedlings.* Seedlings with radicles up to 15 mm long were capable of renewed germination after 19 days of desiccation (air-dry) provided the plumule had not developed enough to be externally noticeable. Adventitious roots developed the second time.

19. *Beginning of viability.* Florets removed from the panicles of *B. tectorum* at the time purple coloration was just beginning to develop were later found viable. Even in plants clipped when entirely green and when starch accumulation had not yet progressed to the "dough" stage, some viable seeds were later found.

20. *Length of viability in storage.* Florets of *B. tectorum* stored for 11.5 years in a paper sack in a laboratory were found to be 96% viable.

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THE CORTICOLOUS COMMUNITIES OF LICHENS AND BRYOPHYTES IN THE UPLAND FORESTS OF NORTHERN WISCONSIN

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INTRODUCTION

The plant ecologists at the University of Wisconsin have for several years been working toward the goal of a broad synthetic treatment of the vegetation of the state. Many stands have been studied throughout Wisconsin and the data collected by all workers who study them are on permanent file.

The aim of the present study is to describe the corticolous (bark-inhabiting) vegetation of the forests of the upland of northern Wisconsin. In view of the general program, this study is concentrated upon those aspects of the corticolous vegetation which will contribute most to the ultimate synthetic study of the whole vegetation; namely, the interrelationships of the bark vegetation and the relationships of the bark vegetation to the arboreal vegetation. Minor idiosynerasies of particular corticolous species, of intense interest to students of the cryptogams but from which few broad generalizations might be drawn, cannot be dwelt upon.

The corticolous communities in northern Wisconsin include lichens, bryophytes, algae, and fungi but no phanerogams. In this study only the lichens and the bryophytes, by far the most conspicuous and most important part of the bark vegetation, have been considered.

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Hale (1955) has made a similar study of the corticolous lichen and bryophyte communities of the southern prairie-forest border province in Wisconsin. Since the methods of data collection which have been used both in his study and in the present one are essentially the same, most of the data are directly comparable. An extensive comparison of the bark vegetation of the two floristically different provinces of Wisconsin, however, exceeds the scope of this paper. Although some contrasts of the vegetations will be made if they are indispensable to an understanding of the northern communities, the problem will be reserved for treatment elsewhere (Culberson 1955) in a synthetic study.

This project was supported by a grant from the Wisconsin Alumni Research Foundation. It is a pleasure to acknowledge the aid of Dr. J. W. Thomson, who supervised the research, and of Dr. J. T. Curtis, who made valuable criticisms. Dr. Margaret Fulford and Dr. H. S. Conard aided with certain taxonomic problems. The author's wife helped with many of the calculations from the basic data.

DESCRIPTION OF THE REGION

The western, northern, and eastern boundaries of the region are set as those of the northern part of the state of Wisconsin itself. The southern boundary of northern Wisconsin has been taken as the southern

FIG. 1. The location of the 70 stands, all of northern forest type by arboreal vegetation, in which the data for the present study were collected. The straight line is the southern edge of Township 28 North; the undulating line, from an unpublished map prepared by Dr. J. T. Curtis, is the average southern limit of 10 northern tree species.

edge of Township 28 North (Fig. 1). The criteria involved in the latter, seemingly arbitrary, choice will be discussed later.

Northern Wisconsin, as delimited above, comprises some 25,500 square miles. Physiographically the region, save the easternmost part, belongs to the Superior Upland Province, an extension into the United States of the Pre-Cambrian Upland Province of Canada. The topography, of modest relief, is controlled in places by the bed rock (plateaus and rounded hills of massive rock) and in others by glacial drift (moraines and outwash plains). By contrast, the extreme eastern part of the state shows a topography of cuestas on resistant formations, for example the Door Peninsula, with much glacial modification.

By climate, northern Wisconsin is classified by Borchert (1950) as belonging to that region of northeastern North America which "is characterized by snowy winters . . . Summers are usually free from severe, protracted drought. Thus deep winter snow and reliable summer rains are the features which set off the climate . . ."

METHODS OF COLLECTING THE DATA

In studies of corticolous populations, invariably it is the individual tree, or some area on it, that must be taken as the basic unit of the sample. The problem then is one of selecting, without bias, the trees to be studied. A method for an unprejudiced selection of trees in a woodlot seems to be admirably provided by the "random pairs" technique, a special transect procedure described by Cottam & Curtis (1949) for the survey of tree vegetations. The random pairs method affords not only an objective choice of trees for cryptogamic study, but it retains its original function of allowing the worker to collect, efficiently and rapidly, sufficient data on the tree composition of the stands for a reliable analysis of the arboreal vegetation.

Every upland stand, of northern forest type, listed in the files of the Ecology Laboratory of the University of Wisconsin was considered potentially suitable for the study of the cryptogamic vegetation, but limitations of both time and research funds did not permit all to be examined. During the summers of 1952 and 1953 as many of the stands as possible were visited. No stands were rejected because the cryptogamic vegetation appeared uninteresting or poorly developed, but three were rejected because logging had gone on between the time of the original tree study (Brown & Curtis 1952) and the time that they were revisited. All of the data were collected in the closed forest and trees at the roadside or in otherwise disturbed habitats have not been considered.

Each of the 70 stands (Fig. 1) was sampled as follows: By the random pairs method a sample of 20 points (40 trees) was made along the several radiating transects started near the center of the woodland to insure the exclusion of trees in the very edge. The points along the paced transect were spaced at an interval predetermined by a consideration of the size of the woodlot and of the spacing of the trees. The interval between the points, although constant within a single stand, ranged from about 10-15 m from stand to stand. For each tree (woody plants with a stem more than 10.2 cm d.b.h.), the d.b.h. was recorded and a "cylindrical" quadrat 35 cm high was used at breast height (1.4 m) for the sample of the cryptogamic vegetation. The quadrats thus varied in size because tree trunks vary in circumference. The question of the validity of data collected from quadrats of variable size, as that question is related to this study, will be discussed later.

In 22 of the stands the cryptogamic vegetation at the base of the trees was also sampled with another cylindrical quadrat from the soil level to a height of 35 cm on the trunk. Of the 2,000 trees sampled for cryptogams at breast height in northern Wisconsin, 880 were also sampled at the base. The actual number of quadrats sampled per tree species is recorded in Table 1.

Inasmuch as *Pinus banksiana* is the only species normally with branches at breast height in the vegetation studied, the cryptogamic populations of the branches were also investigated. All of the branches at breast height were designated as the quadrat. In one stand, however, the jack pines had no branches at breast height.

Samples of each species of lichen or bryophyte occurring in a quadrat were placed together in a small paper bag numbered for identification. No species in a quadrat was left unsampled because it was sterile or poorly developed.

TABLE 1. The 21 species of trees found in the 50 stands studied in northern Wisconsin and the climax adaptation number (C.A. No.) assigned to each species by Brown and Curtis (1952). An asterisk indicates the species which are most frequently stand dominants.

C. A. No.		Number of Quadrats at Breast Height	Number of Quadrats at Base
1	**Pinus banksiana* (jack pine)	120	120
2	*Quercus ellipsoidalis* (jack oak)	11	6
2	**Populus* spp. (poplar)	167	53
3	**Pinus resinosa* (red pine)	124	47
4	*Quercus alba* (white oak)	20	4
4	*Prunus* sp. (cherry)	6	2
5	**Pinus strobus* (white pine)	330	226
5	*Betula papyrifera* (paper birch)	78	37
6	*Acer rubrum* (red maple)	90	34
6	*Picea glauca* (spruce)	2	2
6	**Quercus rubra* (red oak)	125	50
7	*Abies balsamea* (fir)	11	2
7	*Thuja occidentalis* (arborvitae)	1	1
8	**Tsuga canadensis* (hemlock)	283	86
8	*Betula lutea* (yellow birch)	78	30
8	*Fraxinus americana* (ash)	16	6
8	*Tilia americana* (linden)	50	15
8	*Ulmus americana* (elm)	36	10
9	*Ostrya virginiana* (ironwood)	20	5
10	**Fagus grandifolia* (beech)	141	36
10	**Acer saccharum* (sugar maple)	291	108
	Totals	2000	880

All of the data refer to quadrat presence and no attempt to estimate cover was made. Other aspects of the distribution of the corticolous cryptogams were not studied because their measure, like that of cover, would have necessitated unwarranted modifications in the procedure of data collection. For example, it has been shown that, in some corticolous communities, species distribution can be correlated with exposure (Steiner 1952) and likewise an analysis of the vertical distribution of species to great heights on the trunks can provide instructive results (Hale 1952).

All of the taxonomic determinations were made and recorded in the laboratory. Some of the determinations were made at sight, most were made under the dissection microscope, and still others required free-hand sectioning. The data from the 70 stands are based on 20,857 determinations.

Most of the nomenclature of the lichens follows that of Fink (1935) although certain modifications adopted tend to increase its similarity to that of contemporary European usage. The species of only two of the more common lichen genera—*Usnea* and *Pertusaria*—have been grouped under the generic name because the taxonomy is currently so confused that no other treatment is reasonable. A few species names, such as *Cladonia chlorophaea* and *Leconora subfusca,* should be regarded in their broadest sense and the races or the "small species" into which they are commonly divided have not been recognized.

The nomenclature of the mosses is in accordance with Grout (1940) and that of the hepatics with Evans (1940). When random quadrats on trees are studied, much of the sterile or juvenile bryophytic material in certain genera is of such quality that specific determinations are impossible. Of the genera more commonly found, *Brachythecium, Plagiothecium, Orthotrichum,* and *Pylasia* have not been separated to species. Needless to say, the failure to segregate the species of a few genera adds some error to phytosociologic conclusions based on comparisons of numbers of species in particular habitats or on numbers of species per quadrat. Fortunately the only genera unseparated to species in the data for the vegetation at breast height, the major subject of this study, are *Orthotrichum* and *Pylasia,* and both are of relatively low over-all frequency.

Despite the fact that a great effort was made to identify all specimens found, a small collection of lichens of which most were encountered but once, remains unidentified. To illustrate the author's determinations and to provide records for distributional studies, some 1,600 specimens have been deposited in the herbarium of the University of Wisconsin. Summary sheets of all original data at the stand level are on file in the Ecology Laboratory there.

ARBOREAL VEGETATION

That Wisconsin is divided into two floristically different provinces has long been known. Distribution maps of northern and of southern vascular species have been prepared both from reports and herbarium records (McIntosh 1950) and from a quantitative survey of the areas of maximum abundance of species (Lindsay 1953).

The main floristic difference between the upland forests of northern Wisconsin and those of the southern province is that in the former the most pioneer stands, and indeed most of the other non-climax communities, are dominated by conifers. In the southern prairie-forest border province, no conifers exist on upland sites except the infrequent Juniperus, a few stands of jack pine, and some isolated relict stands of white pine. The two provinces are separated by a relatively broad ecotone in which the edge of the range of many northern and of many southern species meet and overlap. The average southernmost limit of the distribution of 10 northern tree species is shown by the undulating line in Fig. 1.

In a detailed study of the upland vegetation of northern Wisconsin, Brown & Curtis (1952) found that in their 116 stands there are "56 different arrangements of the first and second species, 85 different arrangements of the first three, and 105 different arrangements of the first four." From this

evidence it is not surprising that they have not used a system of phytosociologic classification involving the description of a series of communities each characterized by various groupings of the major dominants.

By assuming *Pinus banksiana* to be the most pioneer tree species and *Acer saccharum* the most climax species in the upland vegetation, Brown & Curtis found it possible to place all of the other species in intermediate positions. The relative position that a given species should assume in the arrangement was determined by comparison of the stand by a stand "importance value" (relative dominance, density, and frequency summed) of that species with the importance values of each of the other species in the same stands. The arrangement of species which resulted is essentially an expression of how well adapted each species is, in relation to the others, to participation in the climax sugar maple forest.

On the basis of the established order, a climax adaptation number was assigned to each species. "Tree species which occurred together frequently and hence might be presumed to have nearly similar environmental requirements received nearly similar adaptation numbers while species of widely divergent requirements received widely separated numbers." (Brown & Curtis 1952.) The climax adaptation numbers assigned to the species are given in Table 1 where the most important tree species in the vegetation are marked with an asterisk. Since stands, in which one of the major species is the leading dominant, contain as associates those species with climax adaptation numbers of nearly similar magnitude, a general notion of the series of communities actually present in the northern Wisconsin upland can be formed from a consideration of Table 1.

The system of vegetational classification adopted by Brown & Curtis is an arrangement of stands in a linear sequence in which the relative position of each stand is determined by calculations from the importance value of each of the component species as that value is weighted by the climax adaptation number of the species. Thus every tree species present contributes, according to its importance, to the classification of the community. The exact method of computing the *continuum index* has been described by Brown & Curtis (1952).

PHYTOSOCIOLOGY OF THE CORTICOLOUS VEGETATION

Phytogeographical Delimitation of the Area to Be Included in the Study

In phytosociologic studies of large areas for which the vegetation is evaluated from data on species frequency, a consideration of the floristic homogeneity of the area cannot be overlooked. If, for example, in a certain region picked for study, a group of species are far more abundant in the northern half than in the southern half, then the over-all frequency and constancy values determined for those species will be manifestly influenced by the mere location of the stands sampled. In the present study an attempt must be made to delimit the northern conifer-hardwoods of Wisconsin so that the area defined (1) will not be so large as to be manifestly non-homogeneous from the standpoint of the cryptogamic vegetation and (2) will yet be sufficiently extensive to include enough of the stands sampled to permit adequate phytosociologic analysis.

It was known from observation that the corticolous vegetation in pine stands in the northern part of the state is far richer in species than that in pine stands of the southern part. A study of at least one aspect related to vegetational homogeneity, that of the average number of species recorded per quadrat, might be made from the data collected in pine stands throughout the state. To this end the following procedure was used: Starting with Township 1 North, the southern edge of which forms the Wisconsin-Illinois State Line, the state was divided into a series of parallel east-west bands. Each band is 10 townships (60 mi, 96 km) broad and the width of all four bands is 240 mi. (386 km) (Fig. 2). It should be noted that although a small area of the northernmost part of the state is not included in the most northern interval, the upper limit of the most northern strip is beyond the most northern pine stand sampled.

All stands in which at least 5/8 (25 of 40) of the trees in the sample are jack pine or white pine (either one, not a mixture) were chosen for study. The data from only the jack pines and the white pines were used and those from the minor associated species were not considered. In this way the possible

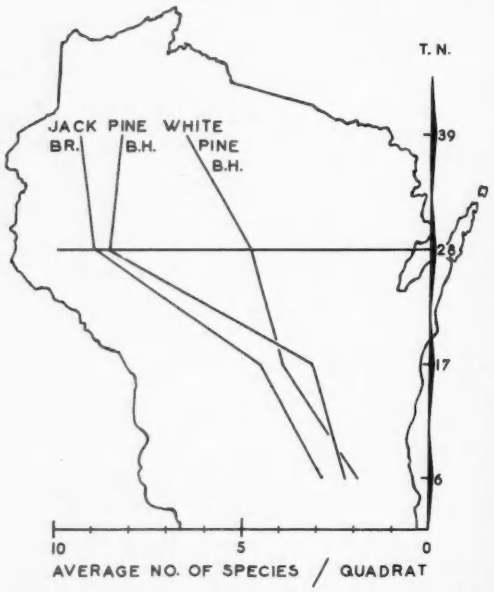

FIG. 2. The average number of species per quadrat on the branches (BR) and on the trunk at breast height (BH) of jack pine and on the trunk at breast height (BH) of white pine in the four geographic intervals.

variables (1) of the influence of the dominant tree species over the corticolous vegetation of all tree species in the stand and (2) of the influence of substrate preference as a factor determining the distribution of cryptogams were eliminated. By dividing the total number of presence records from a single habitat type in a given interval by the total number of quadrats of that habitat type sampled in the interval, the average number of cryptogamic species per quadrat was determined and the datum plotted at the midpoint of the interval (Fig. 2). The number of quadrats of each habitat sampled in each interval is, from south to north: 79, 132, 37, 60 (jack pine at breast height); 79, 101, 37, 60 (jack pine branches); 79, 31, 97, 67 (white pine at breast height).

The corticolous vegetation of white pines in relict stands in the extreme south, and of jack pines in southern stands where jack pine is at the very edge of its range, are both poor in numbers of species per quadrat when contrasted to the vegetation of pines in stands of similar tree composition to the north. Tree species belonging to the northern forests of Wisconsin thus form relatively pure stands in some areas of the state environmentally unsuitable for the development of the rich corticolous vegetation which, in more favorable regions, inhabits their bark.

To see if individual species show similar south to north variations in frequency, the data for several pine-inhabiting lichens common in northern Wisconsin were analyed in a manner analogous to that described for the preparation of Fig. 2. The graph-map of the over-all frequency of *Evernia mesomorpha* in three pine habitats (Fig. 3), very similar to those plotted in manuscript for *Alectoria nidulifera*, *Cetraria ciliaris*, and *Parmelia physodes*, demonstrates again an appreciable south to north variation. The distribution (dots) of all specimens of *E. mesomorpha* in the herbarium of the University of Wisconsin reflects the quantitative occurrence of the species as shown by the graphs, but the dotted map alone is an inadequate representation of abundance.

It should be realized that a constant number of species per quadrat does not alone identify a vegetation as homogeneous, especially if homogeneity is taken as "a distribution of species such that all will be represented with the same probability in each sample of a suitable size" (Curtis & McIntosh 1950). If the vegetation of a single habitat (*e.g.*, the bark at breast height of a tree species) in different regions shows widely divergent average numbers of species per quadrat in those regions, however, that vegetation is not homogeneous throughout its range. In the graph-maps of Figs. 2 and 3, whether the curve concerns the average number of species per quadrat in a single habitat or the frequency in a single habitat of a particular species, the values in the northernmost pair of intervals are far more similar to each other than they are to the values in the southernmost pair of intervals. In this study, where the measure of frequency is to be used alone, to combine indiscriminately the data collected in the southern jack

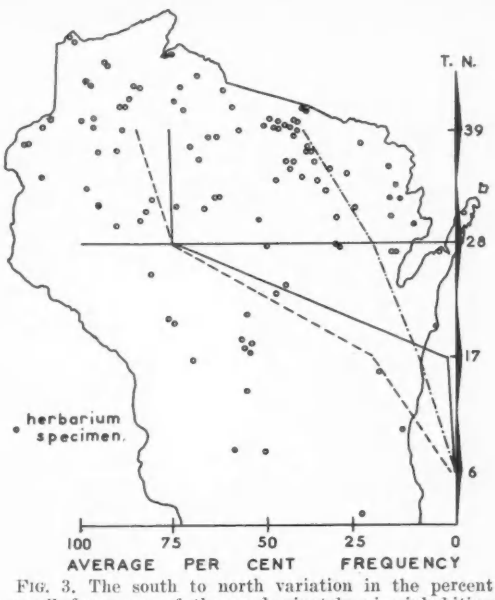

FIG. 3. The south to north variation in the percent over-all frequency of the predominately pine-inhabiting lichen *Evernia mesomorpha* on the branches at breast height of jack pine (- - - -), at breast height on the trunk of jack pine (———), and at breast height on the trunk of white pine (— · — · —).

pine and white pine stands with those collected in the same forest types in the north, merely because the dominant trees in the stands are the same, would introduce an error of such magnitude that the results would reflect accurately the cryptogamic vegetation of neither region.

The most obvious solution would be to define all stands in the northern pair of segments as suitable for the study, but in reality none of the pine stands in the interval of Townships 23-33 North are actually south of Township 28 North, the midpoint of the interval. Instead, 28 North has been taken to be the southernmost township in which stands will be considered for purposes of the phytosociologic investigation. Of the 70 stands sampled, 50 are included in this area. South of the line there are 20 stands from which the data from the 800 quadrats are suitable for purposes of comparison only.

It may be wondered if the corticolous vegetation of nonconiferous trees is subject to a south to north variation in the average number of species per quadrat similar to that of the pines. In the next section it will be shown that in northern Wisconsin, red oak supports an average of about 8 species per quadrat, approximately the number found by Hale (1955) on red oak in southern Wisconsin. The bark vegetation of red oak is then consistently rich in species throughout the state. On the other hand, linden in northern Wisconsin has an average of about 5 species per quadrat as contrasted to 3 in southern Wisconsin; sugar maple has an average of about 7 in the north but of only about 2 in the south (from Fig. 5 and

Hale 1955). For the corticolous vegetation of some species of hardwoods common to the upland vegetation of both provinces, a very appreciable south to north gradient in the average number of cryptogamic species per quadrat could be demonstrated.

It is not proposed that the corticolous vegetation of stands in and north of Township 28 North is entirely homogeneous. Considering the vast extent of this area, it would be very surprising if it were. The elimination of the error that would be introduced if all data from stands of similar arboreal vegetation, regardless of the location of the stands, were pooled is considered here, however, to be far more important to the validity of this study than is the necessary inclusion of the very much smaller error resultant from minor vegetational variations in the region delimited.

Distribution of Numbers of Species: Richness of the Vegetation

It has already been pointed out that although the height of the "cylindrical" quadrats used in this study is constant (35 cm), the area of the quadrat surface is not, because trunks of trees vary in circumference. To discover the effect of increased quadrat size upon the number of species recorded per quadrat, the data from all quadrats on the two most frequently encountered species, *Pinus strobus* (330 quadrats) and *Acer saccharum* (291 quadrats), were studied.

Size classes, based on d.b.h., were set up and the mean and the modal numbers of species per quadrat were determined for the quadrats of each class (Table 2). The data for *Pinus strobus* show no variations that could not be attributed to expected sampling error and for *Acer saccharum* the variation from class to class is neither of a magnitude nor of a trend to permit postulations concerning a constant influence of increased quadrat size on the number of species recorded per quadrat. Similar results in studies of corticolous vegetations have been obtained by Klement (1952) in Germany and by Hale (1955) in southern Wisconsin.

It is not proposed that the above results in any way contradict the well-established fact that quadrat size and number of species per quadrat can be shown to be related. It appears simply that the quadrats in the class of the smallest size used here are large enough to include the same number of species found in the largest quadrats used. Likewise it should not be assumed that individual cryptogamic species must necessarily occur with a constant frequency on trees of all size classes. No analyses of this aspect were made but various groupings of cryptogamic species noted on the trunks of trees of different age have at times been observed and interpreted as the result of succession (Billings & Drew 1938).

The relative richness of the cryptogamic flora of the northern forests as contrasted to that of the forests of southern Wisconsin can be estimated by determining for each region the percentages of the total number of trees sampled in each with a given number of corticolous species. The distribution of the 2,000 trees sampled at breast height in northern Wisconsin and of 2,797 trees sampled at breast height by Hale (1955) in southern Wisconsin is shown in Fig. 4. In the south about 10-11% of the trees are without cryptogams at breast height whereas in northern Wisconsin only 2-3% of the trees have no cryptogams at breast height. The increased richness of the northern vegetation over the corresponding southern one can be appreciated by observing the difference in ranges of the curves.

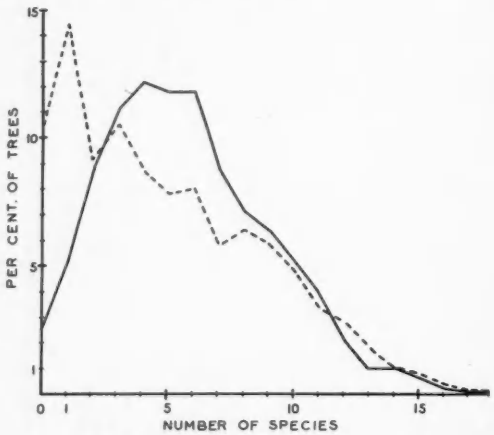

FIG. 4. The percentage of trees with a given number of cryptogamic species at breast height in northern (———) and in southern (-----) Wisconsin.

TABLE 2. The mean and the modal numbers of species per quadrat vs. the size classes of the trees sampled (*i.e.*, vs. quadrat size).

d.b.h. in cm.	*Pinus strobus*			*Acer saccharum*		
	Mean	Mode	No. of Trees	Mean	Mode	No. of Trees
10-20	6.6	6	59	6.2	5	113
20-30	5.8	5	67	7.6	7	83
30-40	6.5	6	89	8.2	9	55
40-50	6.9	6	76	7.4	7	23
50-60	6.5	6	28	7.6	8	11
60 or more	5.7	5	11	6.2	6	6

The greater species richness of the corticolous vegetation of northern Wisconsin is also reflected in the total number of species recorded. Hale (1955) encountered 82 corticolous cryptogams (50 lichens, 32 bryophytes) in the south whereas 123 species (82 lichens, 41 bryophytes) have been found in northern Wisconsin.

To supplement the information in Fig. 4, it would be instructive to know if some tree species support a vegetation richer in corticolous species than others. The data for the vegetation at breast height were analyzed for all trees encountered more than 45 times in the sample of 2,000 trees. The average number of species per quadrat at the base of the same tree

species was also determined, but for some of the species the computation for the basal vegetation was made from a sample of less than 45 quadrats. The number of quadrats involved per tree species ranges from 50-330 for the vegetation at breast height and from 15-226 for that at the base (Table 1).

From a graphic representation of the relative species-richness of the vegetation of the 12 leading tree species (Fig. 5) it can be seen that (1) there is no apparent correlation between a high (or a low) average number of species at breast height and a high (or a low) average number of species at base, and that (2) the order of the trees by descending average number of species at breast height shows no general difference between the species richness of the flora of the conifers and that of the hardwoods. The significance of the latter observation will soon become apparent.

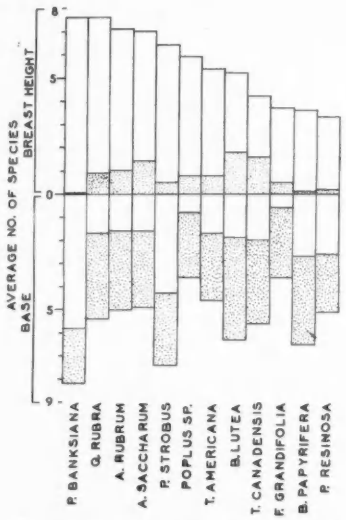

FIG. 5. The average number of crpytogamic species per quadrat at breast height and at the base of the 12 most commonly encountered tree species. The length of the column indicates the average number of cryptogamic species; the shaded part is the portion of the total number which is of bryophytes, the unshaded part of lichens.

THE BASIC DATA

In the section on methods it was pointed out that the only data collected in this study are those of quadrat presence. Thus all of the conclusions will be derived from measures of frequency. That frequency is directly related to density if individuals of the species are at random is known (Curtis & McIntosh 1950).

In Table 3 the over-all frequency (total number of quadrat presence records/total number of quadrats examined $\times$ 100 = x/2,000 $\times$ 100), the constance (total number of stand presence records/total number of stands examined $\times$ 100 = y/50 $\times$ 100), and the percent frequency on the leading tree species are given for the 68 major lichens and bryophytes at breast height, *i.e.*, those species with an over-all frequency of more than 0.7%. Of the 37 species which occurred with an over-all frequency of less than 0.7% (species found in fewer than 14 of the 2,000 quadrats), only 12 were not found also at the base; namely, the lichens *Anaptychia palmatula* Mx., *Bacidia* sp., *Caloplaca* sp., *Leptogium* sp., *Normandina pulchella* (Borr.) Nyl., *Opegrapha varia* Pers., *Parmelia cetrarioides* Del., *P. crinita* Ach., *Physcia syncolla* Tuck., and *Ramalina pollinaria* (Westr.) Ach. and the mosses *Anomodon tristis* (Cesat.) Sull. and *Leucodon sciuroides* (Hedw.) Schwaegr.

Table 4 presents the over-all frequency (x/800 $\times$ 100), the constance (y/22 $\times$ 100), and the percent frequency on the tree species. Again only the species with an over-all frequency of 0.7% or more are included in the table. Aside from the 63 major species, 26 lichens and 8 bryophytes were found in fewer than 7 of the 880 quadrats. These 34 species which are very rare at the base, however, include only 4 lichens, *Cladonia cenotea* (Ach.) Schaer., *C. verticillata* (Hoffm.) Schaer., *Lecidea berengeriana* (Mass.) T. Fr., and *Peltigera canina* (L.) Willd., and 4 bryophytes, *Anomodon rostratus* (Hedw.) Schimp., *Eurhynchium serrulatum* (Hedw.) Kindb., *Hypnum* sp., and *Plagiochila asplenioides* (L.) Dumort., which were not found also at breast height.

Only one moss, *Leskea* sp., and 5 lichens, *Arthonia radiata* (Pers.) Ach., *Lecanora pallida* (Schreb.) Rabh., *Lobaria pulmonaria* (L.) Bir., *Ochrolechia pallescens* (L.) Mass., and *Parmelia trichotera* Hue, occurred at both breast height and at the base of the trees and yet failed to attain an over-all frequency of 0.7% in either habitat.

Now from Tables 3 and 4 with data on the most common species, from the information given above on the rarest species, and from Fig. 5 of the foregoing section, it is possible to make several generalizations concerning the vertical distribution of corticolous lichens and bryophytes in Wisconsin:

1. The number of species of lichens is greater at breast height than that of bryophytes, and the situation is generally reversed in the basal vegetation (Fig. 5).

2. Most corticolous species can be found at both breast height and at the base. Of the 123 species, 79 are found at both levels.

3. Almost all species extremely common at one level are represented at the other. Only 2 of the 29 species with an over-all frequency of 10% or more at either breast height or at the base are restricted to only one level.

4. Although almost all species common in the vegetation of one level are actually found at both levels, most of these species show a definite affinity for one or the other of the levels. Of the 29 species with an over-all frequency of 10% or more at either level, only 10 have a frequency of 10% or more at both levels.

TABLE 3. The percent over-all frequency, constance, and frequency by tree species of the 68 major lichens and bryophytes at breast height. The number following the name of the tree is the number of quadrats examined on that species.

Species of Cryptogams	Over-all Frequency	Constance	*Pinus banksiana* - 120	*Betula papyrifera* - 78	*Pinus resinosa* - 124	*Pinus strobus* - 330	*Tsuga canadensis* - 282	*Acer rubrum* - 90	*Quercus rubra* - 125	*Betula lutea* - 78	*Fagus grandifolia* - 141	*Acer saccharum* - 29	*Tilia americana* - 50	*Populus* spp. - 167
Lichens														
Alectoria nidulifera Norrl.	5.0	38	32	5	4	13	1	..	1	1	..	..	..	..
Allarthonia caesia Fw.	6.4	48	..	13	1	4	1	43	17	2	2	3	4	8
Anaptychia speciosa (Wulf.) Mass.	1.8	38	..	..	..	..	1	..	4	1	..	4	6	7
Bacidia chlorococca (Graewe) Lett.	36.1	84	94	67	74	78	28	41	24	9	9	2	4	11
Bacidia fuscorubella (Hoffm.) Bausch.	2.4	28	..	..	..	..	1	6	2	2	4	10	12	..
Buellia punctata (Hoffm.) Mass.	3.8	24	51	..	1	3	1	1	..	..	1	1	..	1
Buellia stillingiana Steiner	2.6	44	..	1	1	4	..	9	8	..	2	6	..	2
Caloplaca aurantiaca (Lightf.) T. Fr.	0.7	14	..	..	..	..	..	..	..	..	..	1	14	1
Caloplaca cerina (Ehrh.) T. Fr.	4.8	26	..	..	..	..	..	..	..	..	..	..	..	57
Candelaria concolor (Dicks.) Arn.	19.8	66	..	2	..	1	1	22	28	9	13	6	48	17
Candelaria fibrosa (E. Fr.) Müll. Arg.	1.3	18	..	..	..	..	..	..	..	..	..	2	18	6
Cetraria atlantica (Tuck.) DR.	3.7	26	7	..	1	19	1	..	1	1	..	1	2	..
Cetraria ciliaris Ach.	10.0	42	57	1	14	31	3	2	1	..	..	..	..	1
Cetraria fendleri (Nyl.) Tuck.	1.2	6	19	..	..	..	..	..	..	..	..	..	..	..
Cetraria cakesiana Tuck.	0.8	10	..	..	..	..	4	1	..	1	..	1	..	..
Cladonia coniocraea (Flk.) Spreng.	5.8	34	1	2	4	7	23	4	..	1	1	..	24	..
Conotrema urceolatum (Ach.) Tuck.	0.8	18	..	..	..	..	..	..	3	..	1	3	..	1
Evernia mesomorpha Nyl.	17.0	52	69	28	29	40	1	18	14	5	1	1	..	9
Graphis scripta (L.) Ach.	20.7	58	..	..	..	1	22	18	23	64	57	54	18	..
Lecanora subfusca (L.) Ach.	14.0	72	11	5	2	38	1	18	22	1	6	5	2	37
Lecanora varia (Hoffm.) Ach.	7.0	50	40	4	3	18	..	16	2	..	..	1	..	2
Lecidea nylanderi (Anzi) T. Fr.	4.1	16	62	..	5	1	..	..	..	..	..	..	..	..
Lecidea vernalis (L.) Ach.	1.6	26	1	8	..	3	..	6	4	1	..	..	..	1
Lepraria aeruginosa (Wigg.) Sm.	55.4	100	36	35	68	79	84	56	50	67	69	44	24	10
Leptorhaphis epidermidis (Ach) T. Fr.	1.5	24	..	26	..	..	..	2	..	..	..	..	..	5
Lobaria quercizans Mx.	1.0	20	..	..	..	..	..	1	..	1	..	6	..	..
Parmelia andreana Müll. Arg.	1.2	26	..	1	..	4	1	6	2	..	..	..	2	..
Parmelia aurulenta Tuck.	11.6	70	2	..	..	..	1	26	50	15	7	30	24	2
Parmelia caperata (L.) Ach.	28.2	90	42	29	22	76	15	29	40	14	14	5	8	11
Parmelia physodes (L.) Ach.	14.8	50	72	13	30	37	8	7	2	4	1	1	..	2
Parmelia rudecta Ach.	21.4	82	6	5	6	32	43	23	29	27	20	17	20	1
Parmelia saxatilis (L.) Ach.	7.0	58	2	4	2	14	6	10	23	9	1	5	4	2
Parmelia subaurifera Nyl.	12.4	64	11	44	9	13	1	32	27	9	6	7	..	23
Parmelia subquercifolia Hue	7.0	60	..	10	..	4	1	28	40	..	1	4	2	13
Parmelia sulcata Tayl.	23.0	78	67	45	24	36	5	34	43	14	4	6	..	25
Parmeliopsis placorodia (Ach.) Nyl.	2.6	6	43	..	..	..	..	..	..	..	..	..	..	..
Pertusaria sp.	7.6	54	..	1	1	3	4	11	26	8	8	20	6	2
Physcia aipolia (Ehrh.) Hampe	11.0	76	..	..	..	1	1	18	21	..	1	18	42	45
Physcia ascendens Bitt.	0.7	20	..	..	..	..	..	..	..	..	1	1	1	5
Physcia ciliata (Hoffm.) DR.	6.4	46	..	..	..	..	..	1	2	6	..	2	20	64
Physcia grisea (Lam.) Zahlbr.	10.6	68	..	..	..	..	..	8	5	..	..	33	28	27
Physcia millegrana Degel.	5.1	40	..	..	..	1	2	26	9	1	2	14	16	..
Physcia orbicularis (Neck.) DR.	29.4	78	..	1	..	1	1	20	56	37	27	81	84	44
Physcia tribacoides Nyl.	3.6	26	..	..	..	..	..	2	2	..	..	16	14	..
Pyrenula leucoplaca (Wallr.) Körb.	0.9	24	..	..	..	..	..	1	1	..	..	2	6	2
Pyrenula nitida (Weig.) Ach.	1.0	22	..	..	..	..	1	..	3	4	6	1	..	..
Pyxine sorediata (Ach.) E. Fr.	2.0	34	..	..	..	..	1	1	11	2	..	5	2	1
Ramalina fastigiata (Pers.) Ach.	6.9	64	..	1	..	4	1	31	31	..	3	4	..	17
Rinodina halei H. Magn.	4.6	40	..	..	..	..	..	2	9	1	1	22	2	..
Rinodina sp.	1.2	14	..	..	..	..	..	3	9	..	..	1	..	5
Trypethelium virens Tuck.	2.1	8	..	..	..	..	..	..	..	..	30	..	..	..
Usnea sp.	8.4	40	38	17	7	25	2	7	5	1	..	1	..	4
Xanthoria fallax (Hepp.) Arn.	6.0	36	..	..	..	..	..	2	6	..	..	19	28	7
Xanthoria polycarpa (Ehrh.) Rieber	3.4	30	..	1	..	1	..	3	..	..	..	1	..	34
One unknown crustose species	7.5	60	..	1	..	3	1	9	10	8	11	26	12	..
Bryophytes:														
Anomodon minor (Beauv.) Lind.	4.3	44	..	..	..	..	..	2	3	1	1	14	12	..
Dicranum montanum Hedw.	13.8	52	1	1	6	15	68	1	1	23	1	..	..	..
Frullania asagrayana Mont.	4.2	18	..	..	1	3	24	1	..	..	1	..	..	..
Frullania bolanderi Aust.	1.7	16	..	..	..	..	..	6	3	1	6	4	..	1
Frullania eboracensis Gottsche	20.4	92	..	..	..	3	7	20	38	55	14	49	32	25
Lindbergia brachyptera var. *austinii* (Sull.) Grout	4.6	42	..	..	..	1	..	9	4	5	..	12	16	..
Neckera pennata Hedw.	1.8	20	..	..	..	..	12	8	1	10	2	7	..	..
Orthotrichum sp.	2.8	46	..	..	..	..	..	..	1	1	1	3	2	19
Platygyrium repens (Brid.) Bry. Eur.	23.4	86	1	1	2	17	43	30	30	54	18	28	20	3
Porella platyphylloidea (Schwein.) Lind.	2.9	34	..	..	..	..	1	7	..	8	2	10	8	..
Ptilidium pulcherrimum (Web.) Hampe	2.8	28	1	..	6	10	5	..	..	..	..	..	..	..
Pylaisia sp.	2.5	48	..	..	..	..	1	..	..	1	..	7	4	12
Ulota crispa (Hedw.) Brid.	3.4	52	..	..	..	1	1	4	6	13	4	3	2	10

TABLE 4. The percent over-all frequency, constance, and frequency by tree species of the 63 major lichens and bryophytes at the base. The number following the name of the tree is the number of quadrats examined on that species.

Species of Cryptogams	Over-all Frequency	Constance	*Pinus banksiana* - 120	*Pinus resinosa* - 47	*Pinus strobus* - 226	*Tsuga canadensis* - 86	*Quercus rubra* - 50	*Populus* spp. - 53	*Acer saccharum* - 108
Lichens:									
Alectoria nidulifera Norrl.	4.2	36	25	..	2	..	..	..	..
Allarthonia caesia Fw.	0.9	14	..	..	1	..	2	2	1
Bacidia chlorococca (Graewe) Lett.	22.3	68	53	28	48	14	2	2	..
Buellia punctata (Hoffm.) Mass.	3.3	23	22	2	1	..	..	..	..
Candelaria concolor (Dicks.) Arn.	0.9	18	..	..	..	..	4	..	3
Cetraria atlantica (Tuck.) DR.	1.9	14	2	..	6	..	..	..	..
Cetraria ciliaris Ach.	3.5	27	15	2	5	..	..	..	..
Cetraria pinastri (Scop.) S. Gray	4.6	32	21	17	3	..	..	..	1
Cladonia botrytes (Hag.) Willd.	2.2	32	12	2	1	..	..	..	..
Cladonia chlorophaea (Flk.) Spreng.	14.9	59	34	28	24	..	4	9	1
Cladonia coniocraea (Flk.) Spreng.	48.6	91	86	76	78	56	28	32	6
Cladonia cristatella Tuck.	10.8	50	48	6	10	..	..	..	..
Evernia mesomorpha Nyl.	8.2	54	29	2	14	..	..	..	..
Graphis scripta (L.) Ach.	5.8	46	..	..	2	6	6	..	16
Lecanora subfusca (L.) Ach.	3.1	46	2	..	9	..	2	2	..
Lecanora varia (Hoffm.) Ach.	2.0	36	3	4	4	..	..	..	..
Lecidea nylanderi (Anzi) T. Fr.	2.3	14	16	2	..	..	..	..	..
Lepraria aeruginosa (Wigg.) Sm.	36.2	91	14	32	63	85	22	8	15
Parmelia aurulenta Tuck.	1.4	27	..	..	..	..	8	..	5
Parmelia caperata (L.) Ach.	24.5	82	22	15	65	12	6	8	..
Parmelia physodes (L.) Ach.	14.8	59	50	13	22	5	..	..	..
Parmelia rudecta Ach.	11.7	73	4	2	27	10	14	..	7
Parmelia saxatilis (L.) Ach.	1.1	27	..	..	3	..	2	..	..
Parmelia subaurifera Nyl.	1.0	27	1	2	1	..	4	..	..
Parmelia sulcata Tayl.	15.1	73	38	17	22	2	8	4	2
Parmeliopsis ambigua (Wulf.) Nyl.	2.7	18	18	2	1	..	..	..	..
Parmeliopsis hyperopta (Ach.) Vain.	2.6	23	17	4	1	..	..	..	..
Parmeliopsis placorodia (Ach.) Nyl.	1.4	14	10	..	..	..	..	..	..
Physcia orbicularis (Neck.) DR.	12.3	41	..	..	..	3	30	4	52
Rinodina halei H. Magn.	0.7	9	..	..	..	..	2	..	5
Usnea sp.	4.9	46	19	4	6	2	..	..	..
Xanthoria fallax (Hepp) Arn.	4.9	46	..	..	..	..	..	..	4
One unknown crustose species	5.6	23	2	..	1	..	10	..	24
Bryophytes:									
Amblystegium varium (Hedw.) Lindb.	8.9	68	..	..	1	1	16	15	30
Anomodon attenuatus (Hedw.) Hüben	5.2	36	..	..	..	1	4	..	25
Anomodon minor (Beauv.) Lindb.	6.5	41	..	..	..	1	10	2	20
Bazzania trilobata (L.) S. Gray	3.2	18	..	..	2	23	..	..	..
Brachythecium sp.	6.4	41	..	2	3	..	8	70	2
Brotherella recurvans (Mx.) Fleisch.	9.3	68	9	11	11	35	..	..	1
Campylium hispidulum (Brid.) Mitt.	3.0	41	..	..	..	..	14	4	7
Chamberlainia acuminata (Hedw.) Grout	10.8	54	..	..	1	1	24	8	41
Dicranum flagellare Hedw.	22.6	77	60	40	27	12	6	..	4
Dicranum montanum Hedw.	36.1	91	7	21	62	87	10	4	1
Dicranum sp.	1.4	36	4	..	1	..	2	..	1
Entodon sp.	3.5	41	6	2	1	..	14	2	7
Eurhynchium strigosum (Hoffm.) Bry. Eur.	3.8	46	1	2	1	3	12	11	5
Frullania eboracensis Gottsche	23.4	77	..	..	1	1	30	8	38
Heterophyllium haldanianum (Grev.) Kindb.	23.4	77	38	28	25	8	44	9	3
Hypnum reptile Mx.	25.1	84	7	28	33	31	38	19	4
Jamesoniella autumnalis (DC.) Steph.	9.8	73	2	8	15	32	..	4	1
Lindbergia brachyptera var. *austinii* (Sull.) Grout	1.2	32	..	..	1	..	4	..	5
Lophocolea heterophylla (Schrad.) Dumort.	16.2	91	26	21	33	5	6	2	2
Mnium cuspidatum Hedw.	6.2	77	..	..	..	..	22	24	9
Mnium spinulosum Bry. Eur.	2.7	9	..	..	..	10	..	..	2
Neckera pennata Hedw.	2.2	32	..	..	..	..	..	4	8
Plagiothecium sp.	13.8	82	3	13	9	43	14	..	12

Species of Cryptogams	Over-all Frequency	Constance	*Pinus banksiana* - 120	*Pinus resinosa* - 47	*Pinus strobus* - 226	*Tsuga canadensis* - 86	*Quercus rubra* - 50	*Populus* spp. - 53	*Acer saccharum* - 108
Lichens:									
Platygyrium repens (Brid.) Bry. Eur.	30.2	82	1	6	29	48	40	6	57
Porella platyphylloidea (Schwein.) Lind.	8.1	41	..	..	..	..	2	..	41
Ptilidium pulcherrimum (Web.) Hampe	38.3	86	68	64	54	10	12	17	..
Pylaisia sp.	3.1	32	..	..	..	..	2	49	..
Radula complanata (L.) Dumort.	2.8	32	..	..	..	..	..	4	12
Tetraphis pellucida Hedw.	2.2	32	7	4	3	2	..	..	..
Thuidium delicatulum (Hedw.) Mitt.	4.2	41	..	..	..	..	14	8	6

5. Only a very few species are capable of participation in the vegetation of both habitats while remaining very rare in both. Six of the species found both at breast height and at base failed to achieve an over-all frequency of at least 0.7% at either level.

If the data in Tables 3 and 4 are now examined from the point of view of the distribution of the cryptogamic species on the bark of the various tree species, it can be seen that although many of the most common cryptogams can be found at least occasionally on the bark of all tree species, none of them are equally frequent on the bark of all tree species. Each cryptogamic species occurs more frequently on the bark of one or more of the trees than it does on the bark of the others.

METHOD OF PHYTOSOCIOLOGICAL ANALYSIS

With the specific composition of the corticolous vegetation of the major tree species established, the data must now be put into a more understandable form. Because the main aim of this study is to investigate the corticolous vegetation of the different tree species rather than to attempt to examine in detail the distributional interrelationships of individual species of the cryptogams, the problem in effect becomes one of placing the species of trees into a classification by similarity of the corticolous populations they support.

Hale (1955) met the problem of so arranging tree species into an order through a consideration of the distribution of the leading species of cryptogams. By the use of Cole's index, a method of analyzing the intensity of interspecific association, a numerical value was obtained to measure the association of each major cryptogamic species with each tree species. From these values it could be determined whether a given cryptogam is positively, negatively, or randomly associated with a particular tree species. By then comparing the various tree species on the basis of the number of cryptogamic species (with positive indices above a chosen level) that they share, Hale found it possible to rank the trees in an order.

In the present study a somewhat more direct and readily understandable method has been used to ascertain the extent of quantitative floristic similarity among the corticolous vegetations of the tree species.

To determine a *coefficient of community*, a measure of the level of similarity, for any pair of communities from a set of quantitative measurements taken for both, the following procedure is used: (1) To achieve comparable data, all measurements are expressed as precentages (here the percent frequencies of Tables 3 and 4). (2) For each community the percentages are summed. Let the sum of the percentages of the first community be a, of the second b, etc. (3) For the pair of communities, of which a and b respectively are the percentages summed, a summation, w, is made of the lower of the percental values for each species that the communities share in common. Obviously if a species is present in one community and absent from the other, no value for that species is included in the summation w. For a species that occurs in both communities, the lower of the pair of percentages is the one used in the computation of w since that is the quantity actually shared. (4) The coefficient of community is then calculated from the formula

$$\frac{2w}{a + b} \times 100$$

From the very method of computation it can be seen that if two communities have no species in common, the resultant index value is zero, indicative of total dissimilarity, because w, based on species shared, is zero. If two communities are identical, the value indicates 100% similarity (*i.e.*, identity) because $2w$ will equal a plus b. The index thus has a range of 0-100 into which the value for any community, compared to any other, must fall.

The coefficient obtained between a single pair of communities cannot be properly evaluated, however, unless it can be compared with the coefficients between each of the two communities with still others. A coefficient must then be determined for each different pair of communities. For any set of data the number of possible different combinations is

$$\frac{n(n-1)}{2}$$

where n is the number of communities in the study.

The basic method described above for the computation of the coefficient of community was first used in vegetational studies by the Polish botanist Kulczyński (1927). Although Jaccard's somewhat similar coefficient of community (Jaccard 1912) was being widely used on the Continent during the 1920's, Kulczyński's method fell into immediate obscurity. By its use of quantitative data, Kulczynski's method is actually the more appropriate for vegetational analysis whereas Jaccard's index remains the version better suited for comparisons of qualitative floristic similarity. Agrell (1945) adapted Kulczyński's index for testing homogeneity within a community and in so doing provided an interesting means of measuring joint occurrence of species but with the loss of Kulczyński's provision for the incorporation of quantitative data. The Kulczyński coefficient has recently found revived use in Polish phytosociology thanks to its popularization by the lichenologist Motyka (1947) who brought the method to the author's attention. The slightly modified formula for the computation of the index has been given by Motyka and his colleagues (1950).

Theoretically, the coefficient is influenced by each species in the community according to the importance of the species as evaluated by measurement. In effect, however, the species rarest in the whole vegetation contribute insignificantly to the index by their very nature of extreme infrequence. Their contribution is "swamped" as it were by that of the more common species.

To facilitate computations, mimeographed summary sheets by community type (here for the vegetation in the different tree species) were made. Species are listed vertically in alphabetic order and percent frequencies are recorded at the extreme margin of the page. Any pair of communities can then be readily compared by overlapping the appropriate pair of sheets.

The values of the coefficients determined, the communities are placed in an order of similarity to each other by a trial and error method of shuffling the various columns of the coefficients. Generally one must be content with an arrangement of communities in which the coefficients most nearly approximate smooth curves. Although by comparison of the coefficients a perfect classification is rarely realized, the significance of the individual indices as a measure of the level of similarity between given pairs of communities is unaltered. The method is best understood by a consideration of the results derived from its use.

RESULTS AND INTERPRETATION

For the purposes of phytosociologic analysis, the corticolous vegetation of a tree species was taken to be the "composite" community of species occurring with the frequencies recorded in Tables 3 and 4, frequencies computed from the study of many quadrats in many stands. Needless to say, the 39 major lichens and bryophytes recorded for the vege-

TABLE 5. The matrix of values of coefficients of community of the corticolous vegetation at breast height of the tree species encountered more than 45 times in the sample of 2,000 trees.

	Pinus banksiana	*Betula papyrifera*	*Pinus resinosa*	*Pinus strobus*	*Tsuga canadensis*	*Acer rubrum*	*Quercus rubra*	*Betula lutea*	*Fagus grandifolia*	*Acer saccharum*	*Tilia americana*	*Populus* spp.
Pinus banksiana		48	50	57	19	31	27	17	16	11	8	16
Betula papyrifera			66	56	30	50	42	26	26	18	13	29
Pinus resinosa				66	43	42	32	35	35	18	12	21
Pinus strobus					46	50	44	37	35	23	18	26
Tsuga canadensis						42	37	56	48	22	29	14
Acer rubrum							76	52	49	52	45	42
Quercus rubra								56	47	59	49	46
Betula lutea									69	60	44	31
Fagus grandifolia										53	40	27
Acer saccharum											68	36
Tilia americana												42
Populus spp.												

TABLE 6. The matrix of values of coefficients of community of the corticolous vegetation at the base of the tree species encountered more than 45 times in the sample of 880 trees.

	Pinus banksiana	*Pinus resinosa*	*Pinus strobus*	*Tsuga canadensis*	*Quercus rubra*	*Populus* spp.	*Acer saccharum*
Pinus banksiana	....	65	59	26	24	19	9
Pinus resinosa	....	....	72	47	37	30	13
Pinus strobus	....	....	....	57	38	25	16
Tsuga canadensis	....	....	....	....	40	26	24
Quercus rubra	....	....	....	....	....	48	57
Populus spp.	....	....	....	....	....	....	26
Acer saccharum	....	....	....	....	....	....	....

tation at breast height on *Pinus strobus*, for example, were never found all growing together on a single white pine in the field. Instead, the data for the white pine community is a composite constructed from the data from quadrats on 330 trees.

The Kulczyński coefficient has been computed for the different pairs of composite communities. The matrix of values resultant from the analysis of the vegetation at breast hight and of that at the base are given in Tables 5 and 6 respectively. The coefficients have been so arranged that, as columns of figures are read from right to left as well as from bottom to top, the values are in the closest possible descending orders. Thus tree species with a similar cryptogamic vegetation are placed close to each other and farthest away from the tree species from which they differ most in corticolous vegetation.

From Table 5, relative to the vegetation at breast height, these conclusions can be drawn:

1. No pair of tree species have a completely dissimilar cryptogamic vegetation (value of 0) and no pair an identical vegetation (value of 100). The corticolous vegetations of all tree species together form a continuous series.

2. Unlike the arrangement of tree species based on the average number of cryptogamic species per quadrat (Fig. 5), a series which demonstrates no general differences between the corticolous vegetations of the hardwoods and those of the conifers, the present classification does show a very basic dissimilarity in the vegetation of the hardwoods and of the conifers.

3. Although the conifers and the hardwoods are not broadly intermixed along the gradient of vegetational similarity, there is no sharp dividing line between them. The corticolous vegetations of *Acer rubrum* and *Quercus rubra* are intermediate and form a transition between those of the conifers and those of the other hardwoods. For example the vegetation on *Acer rubrum* compared with that on *Pinus strobus*, has a coefficient of community of 50, and with that on *Acer saccharum*, of 52, but the vegetation on white pine and that on sugar maple, compared between themselves, have a value of only 23. The high similarity between the corticolous vegetation of red maple and that of red oak is reflected in their coefficient of community of 76.

4. *Betula papyrifera* is the only hardwood species which supports a bark vegetation more similar to those of the conifers than to those of the other hardwoods.

Populus is the only tree for which the linear arrangement in Table 5 does not appear to reflect best the affinity of its corticolous vegetation. The highest coefficients of the vegetation on Populus are with that on *Acer rubrum* and with that on *Quercus rubra* and yet poplar has been placed at the end of the gradient. The position of Populus should be closer to that of red maple and of red oak, but to put it there would necessitate a separation of tree species which are even more closely related by their corticolous vegetation to red maple and to red oak than is poplar. The highly special vegetation of poplar will be discussed again.

Table 6 presents the results of the analysis of the basal vegetation of the most common forest trees. Although the study of the basal vegetation includes fewer tree species sufficiently sampled for reliable analysis (encountered more than 45 times), all of these species, with the exception of Populus, are found to occupy the same position with respect to each other that they assume by similarity of the vegetation at breast height. In the classification of the basal vegetation, Populus finds position between *Quercus rubra* and *Acer saccharum*, but it must be realized that the perfection with which it is possible to arrange coefficients of community increases as the number of communities in the study is reduced.

The arrangement of tree species in Tables 3 and 4, where the frequencies of the cryptogams are recorded, is identical to the arrangement of the tree species in Tables 5 and 6 respectively. Actually the arrangements in Tables 3 and 4 are the very result of the order achieved through comparison of the coefficients of community (Tables 5 and 6) and these exact arrangements were unknown prior to the present analyses.

From Tables 5 and 6 the reader can find the magnitude of similarity between the corticolous vegetations of any pair of tree species and from Tables 3 and 4 check the actual composition of each community. In a following section the order into which the tree species have been placed by similarity of corticolous vegetation will be used as a basis for the correlation of ecologic data.

SUPPLEMENTARY OBSERVATIONS

The corticolous vegetations of the commonly associated *Pinus strobus* and *P. resinosa* attain a very high level of similarity (coefficient of community = 66), and yet the average number of species per quadrat on white pine is about twice that on red pine (Fig. 5). The reason for the great similarity is clear if one considers the importance of the species actually shared in the corticolous vegetations of the two trees (Table 3). The reason for the appreciable difference in the average number of species per quadrat, how-

ever, is not so immediately obvious. Actually it is due to an entirely physical phenomenon. Unlike the relatively hard and well-attached bark of white pine, that of the red pine is softer, very loosely attached, and is profusely and continually sloughing off during the life of the tree. The cryptogams initiating growth on red pine are literally "shed off" by the tree itself and the corticolous vegetation on red pine rarely develops so richly as that of the particular white pine illustrated in Fig. 6.

Of the 167 Populus sampled at breast height, 131 belong to *P. tremuloides* and 36 to *P. grandidentata*, however for purposes of this study, data from both have been combined. In spite of the fact that in undisturbed stands these species of poplar almost invariably occur as associates of the pines, they display a cryptogamic vegetation very different from that of the pines. The lichens common at breast height on pine are rare on poplar, yet the cryptogams more commonly associated with the more climax hardwoods also fail to reach high frequencies. Instead, *Caloplaca cerina*, Orthotrichum, *Physcia ciliata*, and *Xanthoria polycarpa*, all of which in the upland forests are more or less restricted to poplar alone, from a major part of the vegetation. Thus the corticolous community on poplar does not reach extremes of similarity with that on any of the other trees and the reason for the difficulty of placing this vegetation into a linear classification with others can be understood. The corticolous vegetation of Populus in northern Europe has been described as similarly anomolous (Sernander 1912, Du Rietz 1932).

FIG. 6. A rich development of the vegetation at breast height on *Pinus strobus*. The most conspicuous species are the fruticose *Evernia mesomorpha* and *Usnea* spp. and the foliose *Cetraria ciliaris, C. atlantica, Parmelia caperata, P. physodes, P. saxatilis,* and *P. sulcata*. The crustose species are not visible. The species in the photograph are some of the commonest which inhabit the bark of the conifers in northern Wisconsin.

ANALYSES OF THE BROADER RELATIONSHIPS OF CORTICOLOUS AND ARBOREAL VEGETATIONS

The linear arrangement of northern Wisconsin forest stands, classified by similarity of tree composition and called the continuum (Brown & Curtis 1952), represents both a vegetational and an environmental gradient. This gradient has been demonstrated by positive correlations of data on the trees themselves, the quantitative distribution (behavior) of single species along the gradient, as well as by correlation of data independent of the trees, measurements of physical and chemical characters of the soil and of the distribution of herbs.

The continuum index has, from the manner of computation of the indices of individual stands, a theoretic range of 300-3000. The behavior of a single species in the series of stands along this gradient can be determined by plotting the stand frequency (or some other measure evaluating importance) of the species in each of the stands in the sequence. The resultant curve is a representation of the rôle of the species in the dynamics of the whole vegetation, and stands in the interval of the continuum in which the curve peaks are the ones in which the species becomes dominant or otherwise reaches its maximum importance. Each curve peaks in only one interval of the continuum and the extent to which the curve of a species overlaps those of other species is a measure of the co-existence of that species with the others in stands in which it is an associate rather than a dominant. Behavior graphs for the major tree species have been prepared by Brown & Curtis (1952).

The 50 stands in northern Wisconsin have been ranked in an order by the continuum index of each, as computed from data collected on tree composition at the time that the corticolous vegetation was sampled. The behavior of many cryptogams has been ascertained along this gradient by the following method: For each species the average frequency in each 100-unit interval of the continuum index is determined from the actual percent stand frequencies, based on a 40-quadrat sample per stand, of all of the stands occurring in that 100-unit interval. The resultant series of values are then smoothed once by the running average

$$\frac{a + 2b + c}{4}$$

and the points are plotted directly. The type of modification wrought on original data by the use of the above formula has been discussed by Brown &

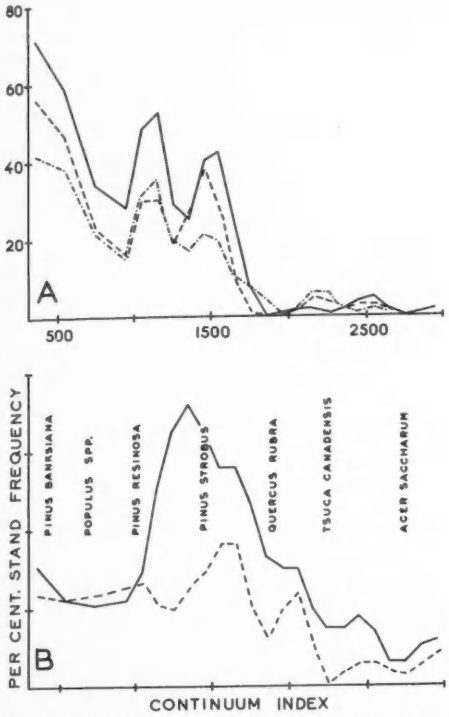

FIG. 7. The behavior of selected cryptogams along the continuum index based on the arboreal vegetation. (A) The lichens *Evernia mesomorpha* (———), *Cetraria ciliaris* (- - - - -), *and Usnea* sp. (— · — · —) all of which are important in the corticolous vegetation of the pines. (B) The lichens *Parmelia caperata* (———) and *Lecanora subfusca* (- - - -) for which the frequency curves peak in the intervals of the continuum index representing stands dominated by white pine or red oak.

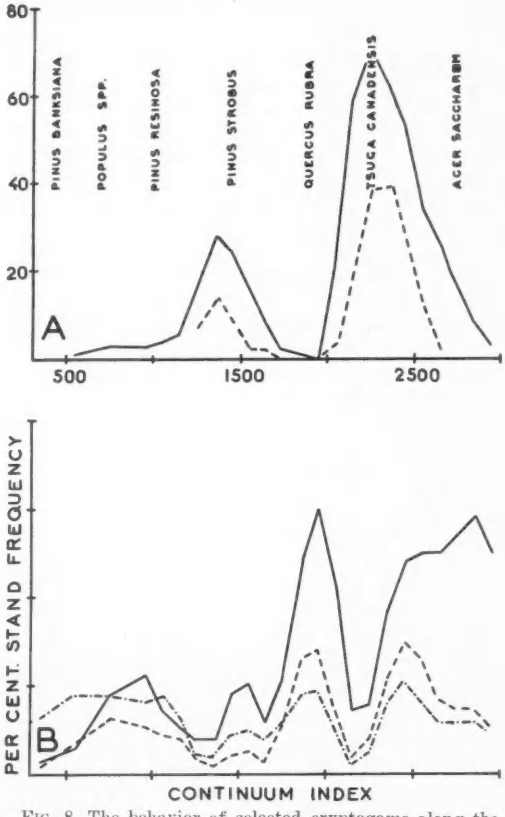

FIG. 8. The behavior of selected cryptogams along the continuum index based on the arboreal vegetation. (A) two bryophytes, *Dicranum montanum* (———) and *Frullania asagrayana* (- - - -), achieving greatest importance in stands dominated by *Pinus strobus* and *Tsuga canadensis*. (B) Three species of *Physcia* with curves reflecting greatest frequency in stands of hardwoods: *P. orbicularis* (———), *P. aipolia* (— · — · —), and *P. grisea* (- - - - -).

Curtis (1952). Actually the method achieved little towards smoothing the curves, but it is doubtless a more objective procedure than that of drawing a free-hand curve through the original points.

Four typical sets of behavior graphs are provided (Fig. 7 and 8). In these graphs the interval along the continuum axis in which each of the major tree species becomes dominant is indicated.

Since the continuum index may be regarded as "a measure of the total environment as expressed by the total tree composition" (Brown & Curtis 1952), then if the behavior of non-arboreal species is determined along this gradient, a positive correlation may be expected (1) to the extent to which the environmental factors which govern the distribution of the trees also govern the distribution of the species in question, and (2) to the extent to which the distribution of the tree species themselves influences that of the non-arboreal species.

The graphs (Fig. 7, 8) show that the entire continuum gradient, from stands which are most pioneer to stands which are most climax, is associated in a very basic way to the distribution of the cryptogams. However, most of the cryptogams display distinctly bimodal curves, a situation which would not exist if their distribution were ideally related to the arboreal continuum. The bimodal nature of the behavior curves is due essentially to the fact that along the gradient some intervals representing stands dominated by hardwoods are separated from each other by intervals of stands dominated by conifers. The basic dissimilarity of the corticolous vegetation of the conifers and that of the hardwoods is one of the major demonstrations of the foregoing section.

Summary sheets of percent stand frequency of the cryptogams were prepared for each of the 50 stands and the Kulczyński coefficient of community was calculated for the 1,225 possible different combinations of pairs of stands. Instead of attempting to arrange the values by a trial and error method, a virtually impossible task, the 50 stands were retained in the order established by the continuum index and thus the arrangement of the coefficients was fixed. From in-

spection of the trend of the coefficients of community it was observed (1) that there is a very great dissimilarity in the corticolous populations of entire woodland stands at opposite ends of the continuum gradient, (2) that the over-all agreement is good in those intervals of the index representing stands that are dominated by tree species shown in the previous section to be closely related by corticolous vegetation, but (3) that if the 50 stands had been placed in a linear order by similarity of corticolous vegetation rather than by arboreal vegetation, a somewhat similar but not identical arrangement of the stands would have resulted.

Before the real meaning of the observations of the foregoing discussion can be properly interpreted, however, the results of a study of some ecologic factors of the bark must be presented.

ECOLOGIC FACTORS OF THE BARK AND COMMUNITY COMPOSITION

The influences exerted by the bark upon the corticolous cryptogams are poorly known and the bark characteristics treated in the literature are those for which measurements can most readily be obtained. Perhaps the most significant studies on the relationships of bark factors to corticolous vegetation in North America have been made by Billings & Drew (1938) and by Hale (1955). Although the greatest effort in the present investigation has been directed towards phytosociological ends, three ecologic factors of the bark—hardness, water absorbing capacity, and hydrogen ion concentration—have been studied.

METHODS

Many bark samples were collected at breast height from the major tree species in the stands. No two samples were taken from a single tree and all were collected on trees supporting a corticolous vegetation.

The bark hardness tests were made under the supervision of Mr. W. G. Youngquist, wood engineer at the Department of Agriculture Forest Products Laboratory at Madison. The apparatus used, the "Presto" hardness tester, is manually operated and gives values that are a measure of the resistance to indentation by steel points attached to a calibrated spring which registers the reading on a dial (Liska 1943). Five hardness tests were made on each of 115 bark samples, and the 5 readings made for each specimen were averaged to provide a single value. Although phytosociologic data for the cryptogamic communities on the two species of *Populus* have been combined in a preceding section, here data on the bark of *P. tremuloides* and of *P. grandidentata* have been recorded separately.

For the determination of the water absorbing capacity of the bark, 89 samples, 10 each from 8 species and 9 from one, each measuring about 4-5 x 9-10 cm, were air-dried for 5 months. The samples were numbered, weighed, coated on all cut surfaces with a thick layer of common household paraffin ("Parowax") applied molter with a brush, reweighed, and submerged in a vessel of distilled water. After 20 hours the specimens were removed, the water remaining on the surface was wiped off, and the samples were immediately reweighed. Calculations of the weight of water absorbed as a percent of the air-dry weight of each of the samples were made.

In the study of the pH, material exterior to the cambium of the individual samples, about 11 per species, was granulated by hand to a texture similar to that of pipe tobacco. Of the pulverized bark of each sample, 3 cc was soaked for 24 hours in 9 cc of distilled water. The pH of the solutions was measured by a Beckman pH meter with a glass electrode and all of the 100 readings, to the nearest tenth, were made in a single run.

RESULTS AND INTERPRETATION

Instead of averaging the data for each tree species, graphic representations of the distribution of the data from each of the three studies were made. From these graphs it is possible to see the entire range of the data for each species and to place the species in orders based on the results of each test.

To illustrate the method used to compare the data of each test, the graph of those from the hardness study has been chosen (Fig. 9) because it appears that no objective investigation of this factor has previously been made in the ecology of corticolous communities. Some authors have implied, however, that the distribution of cryptogams may be related to bark hardness. The assumption is that the hardness and the water absorbing capacity of the bark are intimately related.

Similar graphs have been prepared from the data on the water absorbing capacity and the pH of the bark. The resultant order of tree species by each test is given in Table 7.

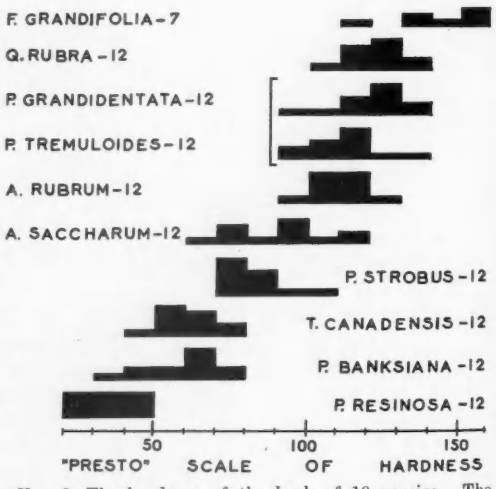

FIG. 9. The hardness of the bark of 10 species. The number following the name of the tree indicates the number of samples tested for the species and the height of the column represents the number of samples which fall in the interval.

TABLE 7. A summary of the relative orders into which the 9 tree species fall by hardness, water absorbing capacity, and pH of the bark, by the "average" ecologic position, and by similarity of cryptogamic vegetation at breast height. The vegetational order is from Table 5 with the omission of the three less frequent species *Betula papyrifera, B. lutea,* and *Tilia americana* for which no bark samples were collected.

	Bark Characteristics			"Average" Position	Vegetational Order
	Hard.	H_2O	pH		
Pinus banksiana	2	3	2	2	1
Pinus resinosa	1	1	3	2	2
Pinus strobus	4	2	1	2	3
Tsuga canadensis	3	6	4	4	4
Acer rubrum	6	7	5	6	5
Quercus rubra	8	8	8	8	6
Fagus grandifolia	9	4	7	7	7
Acer saccharum	5	9	9	8	8
Populus spp.	7	5	6	6	9

The actual values of the weight of water absorbed as a percent of the air-dry weight of the sample range from about 5-95% and the species have been numbered from 1 to 9 by order of decreasing amounts of water absorbed. When the same species are similarly numbered by order of increasing hardness (Table 7), it can be seen that although soft barks tend to have a greater absorptive capacity than hard barks, bark hardness is a crude measure of this aspect of the water relations.

The pH of the bark, which for the entire group of species ranges from 7.0-3.4, provided the arrangement of species (by increasing pH) in Table 7. By doubling and by halving the volume of the sample soaked in 9 cc. of water, it was found that the pH of the solutions from a single bark specimen can vary by as much as 0.5. On the other hand, the order by pH into which a series of samples were placed by one test using a constant volume of the material was the same as the order into which the samples fell in another test using amounts of a different but again constant volume. It appears that if all samples are not of the same volume and are not soaked in a constant volume of water, the pH values are not comparable, but that separate studies, using different but constant volumes of both sample and water, should determine the same relative order of the samples.

If the order of tree species by increasing pH (Table 7) is compared to the order of trees by descending average number of cryptogamic species at breast height (Fig. 5), no apparent relationship between the hydrogen ion concentration of the bark and the species richness of the corticolous vegetation can be found. This observation agrees with the results of Almborn (1953) who has questioned older theories to the contrary.

With the relative order of the tree species established on the basis of the study of three factors of the bark, a hypothetical environmental gradient was imagined along which the bark of each tree species might fall if all of the factors were equally important and if there were perfect compensation. The relative position of each species along the hypothetical gradient is taken to be the average of the positions that it assumes in the three demonstrated series. That an ideal situation of factor compensation probably does not exist and that all factors are not equally important for every corticolous species is of course freely admitted.

But if the order of species in the three series established from studies of the bark and the "average" order of the species along the hypothetical gradient are all compared to the order of the tree species by similarity of corticolous vegetation (Table 7), there can be little doubt that the floristic gradient in the corticolous vegetation at breast height is accompanied by a corresponding ecologic gradient of bark factors. It is probable that if additional ecologic characteristics of the bark had been studied, the "average" order of the trees would have been even closer to that based on their corticolous vegetation. The basic dissimilarity of the conifers and the hardwoods both by corticolous vegetation and by bark characteristics is obvious. The only tree species for which the discrepancy in the "average" ecologic order and in the vegetational order is extremely great is Populus. It has already been pointed out that the rather anomolous bark vegetation of poplar is more like that of *Acer rubrum* and of *Quercus rubra* and its bark characteristics also reflect a greater relationship particularly to those of red maple.

CONCLUSIONS ON THE DISTRIBUTION OF CORTICOLOUS CRYPTOGAMIC COMMUNITIES

It has been shown (1) that the corticolous cryptogams display definite preference of substrate (Tables 3 and 4), (2) that the environmental gradient that accounts for the distribution of the arboreal vegetation appears to be only grossly associated with the distribution of the corticolous vegetation (Figs. 7 and 8), and (3) that the floristic gradient in the corticolous vegetation of the major tree species is closely accompanied by a gradient in the ecologic factors of the bark (Table 7). From these facts it is concluded that, in a region of relatively homogeneous floristics, the most important factors govering the composition of a bark vegetation in the closed forest are factors of the substrate, the bark with which the cryptogams are in intimate contact.

However, a universal explanation of the ecology of the corticolous cryptogams must not be looked for in bark factors alone. Early in this study it was shown, for example, that throughout an extensive region the number of species recorded per quadrat on pine and the frequency of a representative pine-inhabiting lichen are related to the geographic location of the stand in which the trees grow. Here then, apparently, is a phenomenon to be explained by the influence of the known climatic gradient within the

state and there is no question of preference of substrate.

Within more limited regions, a somewhat analogous situation may exist between the corticolous vegetation of a tree and the environment of the stand in which the tree grows. For example, light, necessarily correlated with the series of arboreal communities from pioneer to climax, certainly influences the corticolous vegetation. Although the frequency which a given cryptogamic species can attain even on often-associated tree species may be greatly different because of bark factors, it is not inconceivable that the behavior of that cryptogam may be qualitatively similar on each of the tree species in the stands along the entire environmental gradient of forest communities.

The recognition of bark factors as of primary importance in the distribution of corticolous communities is not a new conclusion. Hilitzer (1925) early arrived at the same conclusion. Members of the Zürich-Montpellier School have classified some corticolous communities by substrate type; for example, the bark vegetation of the conifers falls into the "Cetrarion pinastri association" (Oehsner 1928) named for a species of *Cetraria* common in parts of Europe but infrequent in our region. Hale (1955), in his study of the corticolous vegetation of the southern Wisconsin upland, also concluded that the species of the tree largely determines its bark vegetation. In fact the author has found only one study with apparently contrary conclusions. Phillips' proposal (1951) that "the tree species is not the most important factor in the development and distribution of bark-inhabiting bryophytes in Michigan" is surely correct if the distribution of the species throughout the entire state is considered. His failure to recognize the importance of bark factors within more floristically homogeneous areas, however, can be accounted for by his depreciation and rejection of the methods of collecting quantitative data in phytosociology.

That many crytogams are very sensitive to environmental variations is commonly known. In Europe some workers have even designated lichens and bryophytes as "characteristics" or "differentials" in the description of communities in which the cryptogams play only a minor rôle. This extreme ecologic sensitivity makes the vegetation of lichens and bryophytes an ideal subject for factor analysis. Future research should appropriately be designed to evaluate both the factors most important in the distribution of the cryptogams throughout extensive regions and, in more limited areas, the factors related not only to preference of substrate but also to the more subtle problems of the environment of the whole forest community. The results should at once broaden our knowledge of a little-known group of plants and increase our understanding of the entire vegetation to which the cryptogams belong.

SUMMARY

1. The corticolous lichen and bryophyte communities in 50 stands in the northern Wisconsin upland and in 20 stands of northern forest type in central and southern Wisconsin have been studied by a random sample of 40 trees in each stand. In the 2,880 quadrats in the 50 northernmost stands, 123 species (82 lichens and 41 bryophytes) were encountered.

2. The average number of corticolous species per quadrat on the bark of two species of pine in stands from southern to northern Wisconsin shows a great variation with latitude and the region of northern Wisconsin in which the corticolous vegetation may be presumed to be sufficiently homogeneous for reliable study by conventional methods is delimited.

3. Following a presentation of the basic quantitative data on the frequency of the cryptogams, observations are made on the distribution of species at breast height and at the base of the trunks. The vegetation of both levels share most of the species, nevertheless most of the cryptogams show a definite preference for one or the other habitat.

4. From the frequency distribution of the individual cryptogams on the various tree species, the great importance of substrate preference is clearly shown.

5. Kulczyński's coefficient of community, an index of the level of quantitative similarity of communities, is discussed and is used to place the major tree species into a linear order by similarity of the corticolous vegetation which they support.

6. The order into which the 12 leading species fall in this classification shows a continuous series of bark communities from those of the conifers through the transitional communities on red maple and red oak to the populations on the other hardwoods. An analogous treatment of the data from the less complete sample of the basal vegetation provides corresponding results.

7. If the full range of forest communities from pioneer to climax is studied, an analysis of the behavior of corticolous species in the stands, placed in order by similarity of tree vegetation, shows that the distribution of the lichens and the bryophytes is grossly associated with the environmental gradient which determines the variation in the arboreal vegetation. The general environment of the entire forest stand, however, is not the primary explanation of the distribution of the corticolous cryptogams.

8. The major tree species are placed in three seperate arrangements of relative similarity by quantitative studies on the hardness, the water absorbing capacity, and the pH of the bark. The orders of the tree species by bark characteristics, compared to the order into which the tree species are ranked by similarity of their corticolous vegetation, demonstrates that an environmental gradient of bark factors accompanies the floristic gradient in the series of the bark communities.

9. In the region investigated, where the corticolous vegetation is of relatively homogeneous floristics, the most important factors in the determination of the specific composition of the bark community are factors of the substrate.

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